

Mathematical Modeling of Intraguild Predation and its Dynamics in Ecology

by

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ABSTRACT

A functioning food web is the basis of a functioning community and ecosystem. Thus, it is important to understand the dynamics that control species behaviors and interactions. Alterations to the fundamental dynamics can prove detrimental to the future success of our environment. Research and analysis focus on the global dynamics involved in intraguild predation (IGP), a three species subsystem involving both competition and predation.

A mathematical model is derived using differential equations based on pre-existing models to accurately predict species behavior. Analyses provide sufficient conditions for species persistence and extinction that can be used to explain global dynamics. Dynamics are compared for two separate models, one involving a specialist predator and the second involving a generalist predator, where systems involving a specialist predator are prone to unstable dynamics. Analyses have implications in biological conservation tactics including various methods of prevention and preservation. Simulations are used to compare dynamics between models involving continuous time and those involving discrete time. Furthermore, we derive a semi-discrete model that utilizes both continuous and discrete time series dynamics. Simulations imply that Holling's Type III functional response controls the potential for three species persistence.

Complicated dynamics govern the IGP subsystem involving the white-footed mouse, gypsy moth, and oak, and they ultimately cause the synchronized defoliation of forests across the Northeastern United States. Acorn mast seasons occur every 4-5 years, and they occur simultaneously across a vast geographic region due to universal cues. Research confirms that synchronization can be transferred across trophic levels to explain how this IGP system ultimately leads to gypsy moth outbreaks. Geographically referenced data is used to track and slow the spread of gypsy moths further into the United States. Geographic Information Systems (GIS) are used to create visual, readily accessible, displays of trap records, defoliation frequency, and susceptible forest stands.

Mathematical models can be used to explain both changes in population densities and geographic movement. Analyses utilizing GIS softwares offer a different, but promising, way of approaching the vast topic of conservation biology. Simulations and maps are produced that can predict the effects of conservation efforts.

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Chapter 1

Food Web Theory

We use food webs as limited representations of the interconnected feeding relationships within an ecosystem. The most essential aspect of a food web involves the transfer of energy across trophic levels in an ecological system. All living beings rely on energy for survival, and most are responsible for tracking down their own source of energy through consumer-resource interactions. This manuscript discusses the functions and complex dynamics created from these interactions. We address the various food web configurations that occur because of species interactions, and we focus on intraguild predation, a specific and recurring subsystem of food webs. Intraguild predation occurs because of various species interactions, and it is one of the more complicated subsystems that appears in nature.

One of the most studied areas of food web ecology focuses on equilibrium and stability. This is the basis for mathematical modeling and analysis. From here, we look at conditions for stability and the potential for fluctuations. Another notable aspect is the concurrent fluctuations of populations at large spatial scales. We introduce spatial synchrony, its causes, and its potential to spread across trophic levels.

1.1 Energy Efficiency

All living processes are fueled by energy. Thus, organisms require a constant consumption of energy to carry on necessary biological functions. Energy enters ecosystems as solar energy through primary producers (photosynthesis) at the lowest trophic level. From here, energy flow through a system is governed by the universal laws of thermodynamics. These principles impose constraints on an ecological system that influence the flow and conservation of energy.

Stored energy is available for transfer to species in the next trophic level. However, only a fraction of the energy eaten becomes new body mass. A large portion of the energy

is lost as waste or used by the animal to carry out basic life and internal bodily processes. Thus, an even smaller amount of energy is available to be passed on to the next species. For this reason, higher order trophic species are typically more scarce than those of a lower order because there is less energy to survive on. Energy efficiency limits food web length to about 5 trophic levels (Pimm and Lawton 1977). Since energy sources are not always readily accessible animals will more often than not have multiple food sources, creating a very complex web of directly and indirectly connected species. The transfer of energy between species governs potential species interactions that make up a functioning ecosystem.

1.2 Food Web Dynamics

A wide variety of predator types creates different preferences for energy sources. We know that energy enters a system through primary producers (plants) who get their energy from sunlight. Photosynthesis works in plants to convert light energy into chemical energy that is stored in plant tissue. This stored energy is available for transfer. Herbivores are predators who only "prey" on plants, primary consumers. Carnivores are typically identified as higher trophic order predators where they feed solely on other predators below them. They could be distinguished as those that prey on herbivores (secondary consumers) and those that prey on other carnivores (tertiary consumers). Further complicating potential links, there are omnivores which are predators who feed on both producers and other animals. Parasites are unusual predators that are involved in a consumer-resource with their host (prey). In this relationship, the parasite benefits at the expense of the host, but the host is rarely lethally harmed. Finally, there is a parasitoid that is similar to a parasite but it typically results in the killing of its host.

The mingled species interactions caused by ecological energy efficiency create the complex food webs that we see in nature. All living things are involved in interactions where they are consumed as energy by certain species and in turn consume others for their own net energy gains. Ecological systems exist because of an infinite number of these connections (Ostfeld 1996). Thus, basic food web theory all traces back to the ideas of

connectance (Paine 1988) and energy transfer. We will see later how this idea contributes to the stability of food webs.

In food webs, a link exists between two nodes, or species. Direct links exist between species that are directly affected by the actions of the other, i.e. the effects of a predator on its prey. They can be either positive or negative. Alternatively, an indirect link exists when there is an implied connection between species. It occurs where seemingly separate direct interactions are linked together, typically by a common species. Indirect links can work to inhibit a dominant oscillatory subsystem. However, indirect links and coupled oscillations often complicate systems and make them difficult to analyze via mathematical models. The combinations of all connected direct and indirect links are what make up a complete food web. Most food webs may still remain incomplete due to unrecognizable links between some species.

Mathematic modeling is frequently used to study food web dynamics, and to aid in understanding phenomena that occur in nature. Models are created to describe the dynamics that occur within complex food webs, but they are often simplified to one, two, or three species to facilitate analyses. Models typically include a number of parameters that are used to describe changes in species population growth. When two species interact in nature as predator and prey, these interactions may be included in models with terms that describe the relative effects on growth rate by one species on the other. Ecologists frequently use modeling in their analyses to determine conditions for stability, co-existence, and persistence of multiple species.

1.3 Stability

Food webs help to ensure that one particular species cannot become too dominant, causing an extreme imbalance and possible species extinctions. Ecologists frequently talk about the stability of food webs in terms of persistence in the face of environmental changes. But what does it actually mean for a food web to be stable? Without a certain level of stability, food webs will not be able to exist. Stability typically describes the likelihood that a food

web will remain at equilibrium and the time needed to return to an equilibrium following a disturbance. Consequentially, a stable food web would seem less likely to suffer the extinction of species. This definition of stability is commonly known as persistence (or resilience) and will be discussed.

Previous Work and Theory

The source of food web stability is a central question addressed by food web theory. Common theory suggests that higher complexity and diversity contribute positively to a more stable system. Rooney et al. (2006) propose that the stability of complex food webs depends greatly on the idea of asymmetric coupled fast and slow energy channels. McCann et al. (1998) suggest that the presence of weak interactions help to prevent oscillatory subsystems between strongly connected species and that the most stable system would be comprised of both strong and weak interactions. However, other studies have determined that weak interaction have no effect on the probability of stability (Allesina 2008). There have also been criticisms related to the scale of stability analyses. More recent studies suggest that the traditional local stability analyses are not necessarily sufficient to describe the stability of complex food webs (Chen and Cohen 2001, Krebs 2002, Hastings 1988).

A theoretical explanation describes stability as the absence of population fluctuations (Krebs 2002) However, this only addresses stability at the population level. Is it enough to study a population without considering the dynamics of other closely linked species? Population dynamics are heavily affected by food web structures and thus community dynamics. In this case, it should be necessary to look at stability at the community rather than the population level. This stresses the importance of food web stability in relation to any one particular species. Alan Hastings (1988) acknowledged a similar concern when he questioned the reliability of common stability analyses. He too questioned the spatial scale, population or community level, at which the question of stability should be approached.

Rooney et al. (2006) legitimized their studies by claiming that they could be scaled

to an entire ecosystem if they recognize the fast and slow energy channels to be strong and weak interaction chains. In this case, a top predator is capable of maintaining a stable ecosystem by recognizing changing densities in different energy channels. Since their concept can be used at the ecosystem level they claim that the asymmetry between channels will allow for quick recovery after large perturbations. A fast energy channel allows for quick recovery while a slow channel prevents overshoot dynamics making it essentially impossible to return to the original state (Rooney et al. 2006). Theory suggests stability on a higher level, but there is no empirical data to support this claim. More evidence is needed to make such generalizations (Krebs 2002). Hastings (1988) uses the example of a patch to explain the discrepancies over levels of stability by proposing a population that is unstable at the patch level but stable on a larger scale by means of dispersal and meta-populations.

In addition to spatial scales, there have also been ecologists who question the common use of local stability in stability analyses (Hastings 1988, Chen and Cohen 2001). The mathematical definition of local stability suggests the return to equilibrium after a relatively small perturbation. Unfortunately, when perturbations occur in nature they are typically large (Hastings 1988). It is difficult to pinpoint a set equilibrium in a dynamic system since conditions are constantly changing. Who is to say that there is not also a changing equilibrium? For this reason, is beneficial that ecologists are interested in the persistence of a system where no species goes extinct. Ecologists typically look at persistence in terms of resilience to environmental perturbations.

Chen and Cohen (2001) note that local stability analyses may also exclude some complex dynamics where persistence is possible. They propose that global stability and a study of persistence would be more beneficial to the questions commonly asked about food web (community) dynamics. Local stability analyses could be an appropriate measure for persistence when communities are relatively unchanging, but for communities that are influenced by frequent or large perturbations then global stability is a more accurate means of measurement. Their studies focus on the idea of connectance as the fraction of all possible links that could occur in a food web (Chen and Cohen 2001). Unlike most

theoretical analyses that predict corresponding stability with increased complexity, they conclude that the probability of stability at both the local and global level both decrease with increasing complexity.

There are various ways to consider complexity of food webs. While Chen and Cohen (2001) considered connectance as the basis for stability, Paine (1988) argues that connectance is not an adequate enough concept to base food web theory on. In fact, De Angelis (1975) proposes a number of plausible food webs where increased connectivity does result in an increased probability of stability. Connectivity is calculated from the total number of species present in a food web and the number of observed trophic links (Paine 1988). Complexity, however, can reach far beyond the number of species and possible interactions. The basis for any form of complexity originates from the abundance of food web configurations that occur in nature. These various configurations are formed by different methods and combinations of predation and competition among species. McCann et al. (1998) expand a simple food chain by including a few different three trophic level competition mechanisms that are found in nature into their analyses. The exploitative competition mechanism appears when multiple consumers compete for the same resource, and the apparent competition mechanism is similar with the addition of a top predator feeding on two consumers. Omnivory involves feeding on more than one trophic level and not only different species. Intraguild predation is a specific type of omnivory where a consumer feeds on a basal resource and a second consumer (that feeds on the same basal resource as the first consumer). They also considered inputs from species outside of their target study system.

McCann et al. (1998) measure interactions strengths between species involved in these competition mechanisms in terms of changes in biomass and the preference of one species consuming another. Rather than counting the number of species and the number of potential interactions, they use interaction strengths as a unit for complexity when considering overall food web stability. Results conclude that weak interactions help to prevent oscillatory subsystems between species with strong interaction strengths. For example, the

addition of a second consumer in the apparent competition mechanism works to dampen the initial consumer-resource interaction. This helps to ensure that no species population biomass will oscillate too close to extinction. The presence of the second consumer may increase the predator pressure on the prey species, pushing it closer to extinction. Species typically have multiple prey sources to prevent this. Thus, the presence of weak interactions ensures persistence and overall food web stability (McCann et al. 1998).

Food web stability has been the main area of interest for ecologists studying food web dynamics. It is difficult to pinpoint the exact source of stability because of the complexity of natural ecosystems. Ecosystems are frequently faced with drastic perturbations and disturbances, making it difficult to find a stable equilibrium. The unpredictability of such changes makes a stability analysis even more daunting. Thus, a study centered around an equilibrium is not always the most suitable or realistic. Here, we expand upon the idea of resilience.

Stability vs. Resistance

Holling (1973) defined the term resilience as a measure of the persistence of a system to endure perturbations and to maintain the functional relationships between populations in a community. The persistence of a system suggests necessary conditions to avoid species extinction. More recently, questions of stability have been centered upon this more general concept of persistence. It is possible for a system to have multiple basins of attraction where it will persist as a functional system. Populations have the ability to adapt to rapid or continuous changes in the environment, and their instability in the face of such large perturbations may suggest the importance of their resilience and ability to persist. (Holling 1973). In other words, a system may be decidedly unstable but still resilient.

A resilient system is typically one with multiple basins of attraction where it can persist (Holling 1973, Folke and Carpenter et al. 2004). The occurrence of environmental disturbances frequently causes shifts from one state of attraction to another. As the resilience of a system declines, the probability of a phase shift becomes more likely, and the

system becomes vulnerable to smaller external forces (Folke and Carpenter et al. 2004). Humans have historically had a significant impact on the likelihood of these shifts. Human influence may cause large environmental phase shifts by the removal of whole functional groups of species, alterations to natural disturbance patterns, and impacts on lower trophic species via pollution and climate change (Folke and Carpenter et al. 2004). All of these factors contribute to the loss of resilience that will make an ecosystem more vulnerable to changes.

Some resource management techniques suggest that we must accept the idea of resilience over stability in order to deal with these shifts (Holling 1973). Folke and Carpenter et al. (2004) propose that efforts be focused towards changes that affect resilience rather than trying to prevent uncontrollable disturbances and environmental fluctuations. This is where food web complexity and biodiversity contribute to ecosystem resilience (but not exactly stability). Traditional studies of stability have focused on the much-desired equilibrium. As we saw before, contradicting views argue back and forth about the affects of complexity. However, they neglected to acknowledge the existence of multiple equilibria. It is possible that increased instability results in greater species diversity and complexity and eventually increased resilience (Holling 1973).

Functional groups are made up of species that perform all necessary roles in order for a system to persist, i.e. they occupy a niche. Alterations to these functional groups could cause massive changes to ecosystem functioning (Chapin and Walker et al. 1997). This idea of functionality suggests that a system can persist so long as all roles are occupied. Without a set functional group, the addition or loss of species in an ecosystem may cause drastic structural changes. Studies show that more diverse ecosystems are less susceptible to invasion by exotic species (Folke and Carpenter et al. 2004). Species that are functionally similar but differ in their responses to environmental shifts (functional response) provide the most stability (Chapin and Walker et al. 1997). Loss of these species is of major concern for ecosystem resilience.

The major concern between stability and resilience rests in the applications to re-

source management and environmental control. An approach based on resilience adheres more to the unexpected nature of environmental fluctuations while a stability view focuses on the seemingly unrealistic equilibrium (Holling 1973). As resilience becomes more popular, modeling efforts should lean more towards conditions for species persistence and potential species extinction.

As the focus shifts from a stable equilibrium to a persistent ecosystem, food web configurations still play a significant role in our analyses. One of the more complicated subsystems in a food web is one containing intraguild predation. High diversity and the presence of intraguild predation can help dampen the affects of fluctuations in the environment.

Food Web Subsystems

Since food web dynamics can become extremely complicated and difficult to understand, we can look at smaller subsystems made up of specific species. Subsystems in this case are simply systems that are part of a larger system, a food web. Rather than studying the stability of an entire food web, it could be beneficial to consider the stability of a subsystem. When we look at a limited number of species, it is important to recognize that we will still encounter the same species combinations of interactions that make up a food web. However, depending on the number of species that we are looking at, the number of potential interactions is limited. McCann et al. (1998) proposes a number of different subsystem configurations composed of a variety of species interactions that contribute to structural differences in food webs. These various configurations create interesting differences in subsystem dynamics. Thus, the food web dynamics of our subsystem would depend on the immediate structure surrounding a species (or interaction) that we are interested in. It is typically not enough to look at a two-species subsystem in order to thoroughly understand the factors that are regulating a population. However, we must be careful not to overcomplicated a subsystem in order to facilitate future analyses.

Once a subsystem is identified, we ideally want to find a way to describe it in the

simplest way possible. The most common way to develop a description is through the use of universal concepts and language, mathematics. This is referred to as a mathematical model. It can be used to explain the dynamics of a system (or subsystem in our case), to study the effects of different components or parameters, and to make useful predictions based on the likely behavior of the system.

1.4 Intraguild Predation

Intraguild predation (IGP) is the common focus of food web dynamics since it is one of the more complicated configurations and hence, has more complicated dynamics. IGP describes a three-species interaction where two species that are competing for a shared prey are also involved in a predator-prey relationship with each other. The two competing species are typically termed the IG predator and IG prey where the IG predator feeds on the IG prey, and both the IG predator and IG prey feed on a shared prey. Theory predicts the possibility of species exclusion, competitive coexistence, or even alternative stable states (Holt and Polis 1997). Most ecologists are concerned with conditions for coexistence that will potentially contribute to the stability of an ecosystem. Holt and Polis (1997) theoretically proved that coexistence is only possible when the IG prey outcompetes the IG predator for the shared prey/resource. However, this is where theory and empirical results do not match up. More detailed models can better explain the possibilities of coexistence (Hall 2011).

We study IGP because of the implications that it has on food web stability and resilience. The complexity of an IGP subsystem contributes to the overall complexity of a food web. As the proportion of predators involved in IGP increases, food web stability (or possibly resilience) should also increase (Finke and Denno 2005). IGP also has the ability to dampen the effects that trophic cascades have on drastic environmental shifts (Folke and Carpenter et al. 2004). Mathematical modeling is frequently used to identify conditions for coexistence, extinction, persistence, and stability. Results could significantly benefit the goals of conservation biologists concerned with potential species extinction. Modeling gives us a means of targeting the most influential parameters for biological control. IGP

is extremely prevalent in nature, and a thorough understanding of its direct and indirect effects on food web dynamics would prove extremely beneficial to a better understanding of overall dynamics of a community.

1.5 Mathematical Modeling

The interactions between species in a single food web can become fairly complex and extensive. We can use mathematical modeling to simplify and analyze these interactions. Our focus will be on a three-species subsystem involving both competition and predation, previously explained as IGP. However, modeling efforts began by looking at an isolated, single population. IGP modeling began by exploring the implications of incorporating IGP into pre-existing models for exploitative competition and simple food chains made up of predator-prey relationships (Holt and Polis 1997). Thus, before looking at a detailed explanation and interpretation of IGP it is beneficial to recall basic population equations and how they have developed. Since we are typically looking at changes in population density over time, differential equations are used to describe this rate of change. The first models describing population growth were very simple and excluded all forms of immigration and emigration. We use N as the non-negative population density at a given time, t . Then we can say:

$$\frac{dN}{dt} = B - D \quad (1.1)$$

where B and D represent population natality and mortality respectively. This basic equation can be used to describe an isolated population, but it is extremely unrealistic. Almost all populations experience some sort of immigration and emigration due to other local populations of the same species. If we include methods of dispersal, we get:

$$\frac{dN}{dt} = B + i - D - e \quad (1.2)$$

where additional terms i and e are used to describe changes in population density due to immigration and emigration.

For closed populations, we introduce the per capita rates of natality and mortality, b and d . The per capita rates of change are based on the number of individuals present at a given time. Thus, b and d are the contributions of each individual to the population growth. (b is the number of births per individual at a given time and d is the number of mortalities per individual at a given time). When we consider the rates of natality and mortality dependent on the population density at a given time, then we have bN and dN . To simplify this, we use r as the per capita growth rate, $b - d$. Then we have:

$$\frac{dN}{dt} = bN - dN = (b - d)N = rN \quad (1.3)$$

where a positive r represents a growing population, and a negative r is a declining population. This is the common exponential growth model. If unrestrained, the exponential growth model could be used to describe an expected population density. However, it is not likely for a population to be able to grow without restraints. This would imply unlimited resources and no negative impacts from predators. None the less, it is useful to understand the potential of a species to grow. Some strong invasive and non-native species, especially plant species, may have the capacity to grow exponentially. However, a spatial and/or resource limit will always be reached.

Many outside factors exist that will cause a limited exponential growth. In fact, another common population growth model proposes an upper limit, or carrying capacity. The result is the logistic growth model (Verhulst 1845). This well-known model is recognized by its S-shaped sigmoid curve. Populations that adhere to a logistic growth will initially grow exponentially until they reach their carrying capacity where their growth rate will eventually slow down. Consider carrying capacity K as the limiting factor, then the logistic growth function can be written as:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \quad (1.4)$$

where K will be reached when $r > 0$.

Population limiting factors that influence K can be both density dependent or density independent. When density dependence occurs, the per capita growth rate depends on the current density of a population. It seems logical to assume that a higher density will have a negative effect on growth rate. However, positive density dependence may also occur. This is commonly known as the Allee effect (Allee 1931). This usually occurs when individuals work together while avoiding predation, caring for young, foraging, etc. Competition among members of the same species, and more specifically the same population, is referred to as intraspecific competition. This type of competition results from competition for limited resources. Resources may be shared equally among individuals (exploitative competition), and all individuals will suffer during a shortage. Other circumstances may favor some individuals over others, and resources will be shared unequally (interference competition). This is a sort of "survival of the fittest" where there are winners and losers when resources run short. These types of intraspecific competition will act to limit population density.

The exponential growth equation and logistic growth equation can be used to describe basic population dynamics. However, it very rarely occurs in nature that a population can exist without interactions with other species. By definition, a population is a part of a larger community or ecosystem of species that are all interacting with each other to some degree.

The Lotka-Volterra predator-prey equations are the first to deviate from the widely accepted logistic equation that we already looked at. It is the simplest model of predator-prey interactions. Lotka (1925) and Volterra (1928) assumed that population densities responded to changes based on the product of their biomass densities. This is known as "mass action":

$$\begin{aligned}\frac{dN_1}{dt} &= rN_1 - pN_1N_2 \\ \frac{dN_2}{dt} &= cpN_1N_2 - dN_2\end{aligned}\tag{1.5}$$

where N_1 and N_2 are the population biomass densities of prey and predator respectively. We use r as the per capita growth rate of the prey independent of the predator. Then p is the predation rate, c is the conversion rate of consumed prey to new predators, and d is the external mortality rate of the predator.

But what do these equations mean? Prey species, N_1 , grows at an exponential rate, rN_1 in the absence of a predator. In other words, the prey population would grow uncontrollably and independent of density. pN_1N_2 is the mass action, meaning that the predation rate is a linear function of their masses. This is more commonly known as the predator's functional response, the rate at which a single predator kills its prey (Holling 1959). The linear relationship between predator and prey described here is a simple type I functional response. Functional response will be discussed more in depth later. When we multiply this mass action by a ratio c , we get the amount of biomass that is converted to increased predator biomass (births). This is the numerical response of predators to prey. Holt and Polis (1997) based their model of IGP on this system of equations. If we consider P , G , and M as the shared prey, IG prey, and IG predator respectively then their equations are as follows:

$$\begin{aligned}\frac{dP}{dt} &= P\left(r\left(1 - \frac{P}{K}\right) - a_m M - a_g G\right) \\ \frac{dG}{dt} &= G(b_g a_g P - \alpha M - d_g) \\ \frac{dM}{dt} &= M(b_m a_m P + \beta \alpha G - d_m)\end{aligned}\tag{1.6}$$

where r is the per capita growth rate of the shared prey; K is the carrying capacity of the shared prey; a_i is the effects of the functional response of predator i to the shared prey; α is the functional response of IG predator to IG prey; b_i is the conversion of resource consumption into reproduction for species i ; β scales the benefit of IG predator from IG prey; d_i is the density-independent mortality rate of species i . Their model incorporates a basic type I functional response of predator to prey. We will use their framework to develop our own model for a specified subsystem with more complicated dynamics.

1.6 Spatial Synchrony

Spatial synchrony is a common phenomenon where species population fluctuations occur concurrently in different locations (Hanski and Woiwod 1993). Patrick Moran first proposed this idea that outside factors can synchronize fluctuations among spatially separated populations (Moran 1953). Moran studied the oscillatory pattern of the lynx across all of Canada. He realized that peaks occurred simultaneously in different geographic areas. Synchronizations were not due to a lag effect where peaks in population densities in one area would spark a peak in an adjacent, but disjunct, space. (Moran 1953) Moran concluded that the findings of his studies were consistent with the idea that weather is the main synchronizing agent for lynx populations, typically termed Moran effects. However, it is difficult to tell if there is some other natural phenomenon causing it. Synchronized fluctuations like this occur over a wide range of populations and environmental conditions. Large spatial scales typically make it difficult to identify the precise causes (Abbott and Dwyer 2008, Schaubert 2000). Haynes et al. (2009) studied the transfer of spatial synchrony across trophic levels via predator-prey interactions. Ecologists identify mast seasons when there is a peak in plant seed production. Questions arise about why these masting seasons vary among years and how they are synchronized among populations. Effects extend beyond directly linked species to spark other species synchronizations and possibly outbreaks (Schauber 2000, Haynes et al. 2009)

A popular crop that experiences masting seasons is the acorn. Masts occur every 4-5 years and are believed to indirectly cause outbreaks in gypsy moth populations (Elkinton et al. 1996, Schaubert 2000, Ostfeld 2006, Haynes 2009). Gypsy moths are a major source of forest defoliation in the Northeastern United States. The white-footed mouse, a common predator of the gypsy moth, relies on acorns for energy intake. This three-species system made up of gypsy moths, white-footed mice, and acorns (oak) can be categorized as an IGP subsystem. High defoliation frequencies have ignited a region-wide goal to slow the rate of gypsy moth expansion. Management efforts are based on the analysis of geographically referenced data that is processed with the help of Geographic Information Systems (GIS).

The spatial synchrony and increasing expansion of this system will be discussed more in Chapter 4.

MODEL DERIVATIONS

We have already discussed the general complexity of food web dynamics. Here, we limit our investigation to a smaller subsystem to facilitate analyses. A number of different configurations can be used to describe subsystems, but intraguild predation (IGP) is one of the more complex food web configurations, involving both competition and predation. This combination proves to create an excess of interesting dynamics that can be identified with the help of mathematical modeling. Recent analyses have prompted a greater interest in IGP as a tool for conservation biologists. Ecologists like Lotka (1925) and Volterra (1928) derived two-species predator-prey equations that were later expanded to include three species and eventually intraguild predation (Holt and Polis 1997). We base our model derivations for continuous, discrete, and semi-discrete time series on these equations.

2.1 Food Web Modeling

McCann et al. (1998) predict that food web persistence will be more likely when strong consumer-resource interactions are inhibited by the presence of weak interactions. They study how interaction strengths prevent oscillatory subsystems of complex food webs, and propose that weak interactions act to inhibit oscillations. If we zoom in on a diagram of a food web that shows all links between species, we will begin to recognize different patterns of species connections. We refer to these patterns as food web configurations, and the simplest ones are typically made up of three or four species. Different configurations have different effects on inhibiting oscillations. McCann et al. (1998) develop a model based on species interactions and preferences that can be used to represent a wide variety of configurations by using appropriate parameter values. Their model is as follows:

$$\begin{aligned}
 \frac{dR}{dt} &= R \left(1 - \frac{R}{K}\right) - \frac{\Omega_{C_1 R} x_{C_1} y_{C_1} C_1 R}{\Omega_{C_1 R} R + (1 - \Omega_{C_1 R}) C_2 + R_0} - \frac{\Omega_{C_2 R} x_{C_2} y_{C_2} C_2 R}{R + R_0} \\
 \frac{dC_1}{dt} &= -x_{C_1} C_1 \left(1 - \frac{\Omega_{C_1 R} y_{C_1} R + (1 - \Omega_{C_1 R}) y_{C_1} C_2}{\Omega_{C_1 R} R + (1 - \Omega_{C_1 R}) C_2 + R_0}\right) - \frac{\Omega_{PC_1} x_{P} y_{P} C_1 P}{\Omega_{PC_1} C_1 + (1 - \Omega_{PC_1}) C_2 + C_0} \\
 \frac{dC_2}{dt} &= -x_{C_2} C_2 \left(1 - \frac{\Omega_{C_2 R} y_{C_2} R}{R + R_0}\right) - \frac{(1 - \Omega_{PC_1}) x_{P} y_{P} C_2 P}{\Omega_{PC_1} C_1 + (1 - \Omega_{PC_1}) C_2 + C_0} - \frac{(1 - \Omega_{C_1 R}) x_{C_1} y_{C_1} C_1 C_2}{\Omega_{C_1 R} + (1 - \Omega_{C_1 R}) C_2 + R_0} \\
 \frac{dP}{dt} &= -x_P P \left(1 - \frac{\Omega_{PC_1} y_P C_1 + (1 - \Omega_{PC_1}) y_P C_2}{\Omega_{PC_1} C_1 + (1 - \Omega_{PC_1}) C_2 + C_0}\right)
 \end{aligned} \tag{2.1}$$

where R is resource density, C_1 is the density of the first consumer species, C_2 is the density of the second consumer species, and P is the density of the top predator. They based their equations on an interpretation of the Rosenzweig-MacArthur equations based on energy flow through a system (Yodzis and Innes 1992). Then K is the resource carrying capacity, R_0 and C_0 are the half-saturation densities of the resource, R , and consumer, C_1 , respectively; x_i is the mass-specific metabolic rate of species i ; y_i is the measure of ingestion rate per unit metabolic rate of species i ; and Ω_{ij} is a fraction indicating the preference of species i for consuming species j .

By varying the preference parameter, Ω_{ij} , the equations are altered to describe a number of different subsystem configurations. See Figure (2.1). McCann et al. (1998) use these alterations to study the dynamics of naturally occurring subsystem structures in food webs. We are specifically interested in configuration **e**, IGP, but we will use a different approach in our model derivation.

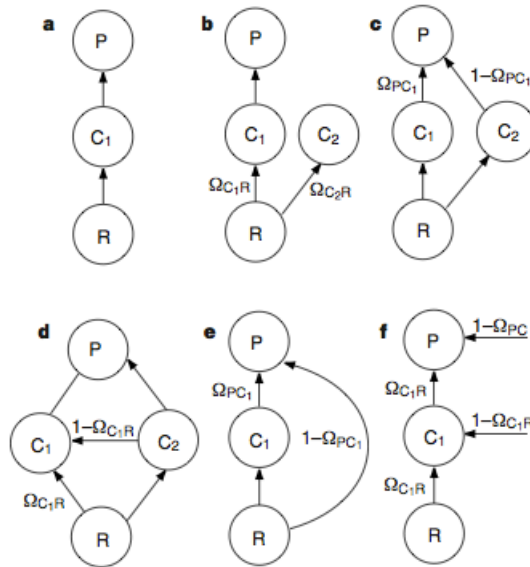


Figure 2.1: Six food web configurations: a) a simple food chain, b) two intermediate consumers competing for the same resource (exploitative competition), c) top predator feeds on both intermediate consumers (apparent competition), d) one consumer feeds on both the basal resource and a second consumer (intraguild predation) plus an additional top predator that feeds on both intermediate consumers, e) intraguild predation (omnivory), f) food chain with external energy sources (McCann et al. 1998)

Intraguild Predation Modeling

Rather than developing a general set of equations that can be adjusted to describe different subsystem configurations, Holt and Polis (1997) took the standard Lotka-Volterra predator-prey model and incorporated IGP into it. We will use P , G , and M as the shared prey, IG prey, and IG predator respectively:

$$\begin{aligned}\frac{dP}{dt} &= P(r(1 - \frac{P}{K}) - a_m M - a_g G) \\ \frac{dG}{dt} &= G(b_g a_g P - \alpha M - d_g) \\ \frac{dM}{dt} &= M(b_m a_m P + \beta \alpha G - d_m)\end{aligned}\tag{2.2}$$

where r is the per capita growth rate of the shared prey; K is the carrying capacity of the shared prey; a_i is the effects of the functional response of predator i to the shared prey; α is the functional response of IG predator to IG prey; b_i is the conversion of resource consumption into reproduction for species i ; β scales the benefit of IG predator from IG prey; d_i is the density-independent mortality rate of species i .

Holt and Polis (1997) explored five equilibria that followed from their new system of equations for IGP:

- (i) All species are at zero density
- (ii) The shared prey is present at density K , but the IG predator and IG prey are absent
- (iii) Only the shared prey and IG prey are present with equilibrial densities of $\frac{d_g}{a_g b_g}$ and $(\frac{r}{a_g})(1 - \frac{d_g}{a_g b_g K})$ respectively.
- (iv) Only the shared prey and IG predator are present with equilibrial densities of $\frac{d_m}{a_m b_m}$ and $(\frac{r}{a_m})(1 - \frac{d_m}{a_m b_m K})$ respectively.

(v) All species exist with equilibrial densities as follows:

$$\begin{aligned} P^* &= \frac{K(r\alpha\beta + a_m d_g \beta - a_g d_m)}{D} \\ G^* &= \frac{(K a_m a_g b_g d_m + d_m r \alpha - K a_m^2 b_m d_g - K a_m b_m r \alpha)}{\alpha D} \\ M^* &= \frac{(K a_m a_g b_m d_g + K a_g b_g r \alpha \beta - K a_g^2 b_g d_m - d_g r \alpha \beta)}{\alpha D} \end{aligned} \quad (2.3)$$

where

$$D = K a_m a_g (b_g \beta - b_m) + r \alpha \beta \quad (2.4)$$

Parameter values determine the existence of equilibria. Furthermore, the existence of some equilibria requires that others be unstable, allowing species that are not present to invade. Holt and Polis (1997) also explore the potential for alternative equilibria or unstable dynamics when (v) is locally unstable.

There are a number of conditions that will determine the stability of the equilibria. Holt and Polis (1997) discuss these conditions for each of there equilibrium. For instance, positive carrying capacity, K , implies that equilibrium (i) will be unstable. We know this is true because K cannot be realistically negative. Thus, Holt and Polis (1997) assume this to be true for all future references.

Equilibrium (ii) is stable when neither the IG predator or IG prey can survive on only the shared prey. If this is true then no other equilibria may exist. However, there are three ways in which equilibrium can be unstable: 1) IG prey can invade, $K > \frac{d_g}{a_g b_g}$; 2) IG predator can invade, $K > \frac{d_m}{a_m b_g}$; 3) both inequalities hold, so either IG prey or IG predator can increase when rare and the shared prey is present at K .

Equilibrium (iii) exists only if the IG prey can invade when the shared prey is at a density of K , and it is stable with respect to to small changes in densities. The condition for this equilibrium to be unstable due to invasion by the IG predator is:

$$a_m b_m \left(\frac{d_g}{a_g b_g} \right) + \alpha \beta \left(\frac{r}{a_g} \right) \left(1 - \frac{d_g}{a_g b_g K} \right) - d_m > 0 \quad (2.5)$$

where there is some value of a_g above which the IG predator will be excluded when rare. On the other hand, increasing growth of the shared prey will ease invasion by the IG predator.

Equilibrium (iv) exists so long as the IG predator can invade when the shared prey is at a density of K , and it is stable to perturbations in either shared prey or IG predator densities. The condition for this equilibrium to be unstable due to invasion by the IG prey is:

$$a_g b_g \left(\frac{d_m}{a_m b_m} \right) - \alpha \left(\frac{r}{a_m} \right) \left(1 - \frac{d_m}{a_m b_m K} \right) - d_g > 0 \quad (2.6)$$

where for any given set parameter values, there is some value of r for the shared prey above which the IG prey will be excluded by the IG predator.

Finally, equilibrium (v) exists in two distinct states where either $D > 0$ or $D < 0$. The local stability analysis done by Holt and Polis (1997) suggests that if the three-species equilibrium exists and $D < 0$ then the equilibrium is locally unstable. Simulations suggest that when the system is nudged from this equilibrium and $D < 0$ that it will converge to one of two boundary equilibria: IG prey exists alone with shared prey or IG predator exists alone with shared prey. Contrarily, if the three-species equilibrium exists and $D > 0$ then either the IG predator or IG prey can invade when rare and the other two species are at equilibrium. Holt and Polis (1997) observe limit cycles of small amplitude on the boundaries of stable and unstable coexistence and much larger fluctuations within the unstable region.

Holt and Polis (1997) showed the potential for alternative stable states where the shared prey is present with either only the IG prey or IG predator along with the increased likelihood of unstable population dynamics with systems involving IGP. Their theoretical analyses led them to develop the coexistence criterion: coexistence is possible when the IG prey is the superior competitor for the shared prey over the IG predator. However, IGP is extremely prevalent in nature, leading ecologists to believe that this criterion is not necessarily true in nature (Arim and Marquette 2004).

2.2 Intraguild Predation

Competition and predation have commonly been recognized as important factors in community ecology. They have long-since been the building blocks of complex, multispecies

food webs (Holt and Polis 1997) that help maintain community structure. Ecologists more recently began to acknowledge an interaction between the two where potentially competing species are also involved in a predator-prey relationship. Holt and Polis (1997) thus define IGP to be this mixture of competition and predation. Species were no longer thought to be limited to either predator-prey relationships or competition between and/or among species. IGP is essentially the hunting of a prey species by a predator that also shares a common, potential resource with this prey species (Holt and Polis 1997). Since both the predator and prey can utilize the same resource, they are in constant competition with each other. The predator species experiences gain in energy from the prey species while simultaneously reducing competition for a resource. The prey species also experiences this reduced competition. McCann et al. (1998) ignited an interest in more complicated food web configurations, suggesting that complexity promotes stability. They propose one specific case, omnivory, where a consumer feeds on resources from different trophic levels, i.e. a basal resource and a second consumer (McCann et al. 1998). IGP is a specific case of omnivory (McCann et al. 1998) with the addition of competition for a shared resource.

The simplest form of IGP involves three species: IG predator, IG prey, and shared prey. The IG prey feeds on only the shared prey while the IG predator feeds on both the IG prey and the shared prey. This three-species system can be seen in Figure 2.2. Common theory proposes that the coexistence of species involved in IGP is only possible when the IG prey is a superior competitor of the shared prey (Holt and Polis 1997). If this were true then IGP would not be observed in nature as often as it is, and recent analyses suggest that IGP is extremely prevalent (Arim and Marquet 2004). Many studies have been done that look at the discrepancies between theory and empirical data. Rather than studying theories that do not adhere to nature, scientists must continue to analyze the dynamics of systems that do involve IGP.

Continued interest in IGP could lead to breakthroughs in conservation biology. IGP has been a recurring theme in community ecology, but it has not been thoroughly studied until recently. Studies of community ecology begin at the simplest level, two or three

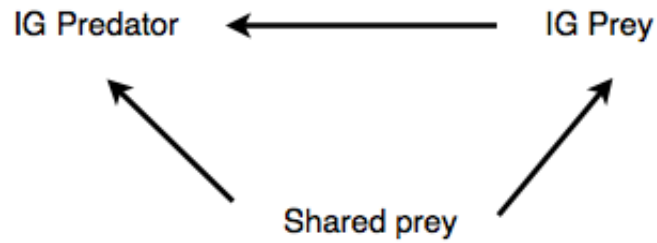


Figure 2.2: Basic asymmetric intraguild predation diagram where the IG predator feeds on both the IG prey and the shared prey, and the IG prey feeds on only the shared prey. Arrows represent the direction of energy transfer across or within trophic levels.

species. A three-species IGP system is relatively complex and can serve as the building blocks to study even more complex systems.

Generalist vs. Specialist Predators

Increased interest in biological control among insects has led ecologists to investigate the various characteristics that constitute a good control agent. Ecologists specified predators that have a high degree of prey specificity, a short growth period relative to the prey, and high female fecundity to be the best control agents (Snyder and Ives 2003). Most biological systems, including those involving IGP, are comprised of a wide variety of predators: generalist and specialists. Generalist predators typically survive on a wide variety of prey, giving themselves a sort of environmental buffer when resources begin to run short while specialist predators have a much narrower diet and require more specific environmental conditions. Thus, parasitoids are often seen as good sources of biological control, and they are frequently used in ecological studies. They possess all of the traits believed to be most effective, and they have proved to be beneficial after intentional introductions to control pest populations (Snyder and Ives 2003). However, there is also evidence that parasitoids have failed to regulate pest populations (Brodeur and Rosenheim 2000). Generalist predators typically poses none of these traits. Undeterred by this, they have repeatedly been reported as successful agents for biocontrol (Snyder and Ives 2003).

Ecologists have studied the impacts of generalist vs. specialist predators separately

along with the potential outcome of interactions between them (Snyder and Ives 2003, Hassell and May 1986, Hanski and Hansson et al. 1991) in various environments. They specifically question whether generalist and specialist predators work additively or against each other to control prey (host) populations among insects (Snyder and Ives 2003). In their study of parasitoids, generalist predators, and aphids Snyder and Ives (2003) found that biological control was most effective for their experiment when both parasitoids (specialists) and generalist predators were present, but the effectiveness of each varied over time. It may happen that parasitoids and generalists begin to work against each other over a longer time scale. Thus, time may be an important agent in biocontrol. Other studies address the addition of a specialist predator to an existing two-species generalist-prey system (Hassell and May 1986). While considering the life cycle of their experimental prey, Hassell and May (1986) compare models where (1) the specialist comes before the generalist in the host's life cycle and (2) the specialist comes after the generalist in the host's life cycle. They found that the specialist has a better chance of successful invasion and persistence when it precedes the generalist. Again, time is an important factor. Unfortunately, three-species systems offer a wide array of dynamics, and they are highly dependent on various parameter values along with the host's life cycle (Hassell and May 1986).

The use of both specialist and generalist predators in biological control depends on a number of different parameters, and it can exhibit sometimes extreme dynamics. Ecologists believe that the ability of predators to suppress prey populations may depend critically on the presence of intraguild interactions. Here we will consider two three-species systems containing an intraguild predator, intraguild prey, and shared prey where the intraguild predator is 1) generalist predator that feeds on both the intraguild prey and shared prey along with outside resources, and 2) specialist predator that feeds only on the intraguild prey and shared prey.

Trophic Cascades

Human influence has many negative impacts on fluctuations in the environment. One of these is caused by overexploitation of top-predator species (top down effects), and another

is caused by pollutants and other dangerous activities leading to the destruction of valuable basal resources (bottom up effects) (Folke and Carpenter et al. 2004). After endless years of taking advantage of our natural environment, we have notably decreased the capability of ecosystems to deal with these changes.

A "top down" trophic cascade occurs when a food web is disrupted with the removal of a higher order consumer. The removal of a top predator releases their prey from their predatory effect. A "bottom up" cascade occurs when a primary producer or consumer is removed causing a diminished population size throughout the community. Trophic cascades caused by these top down and bottom up effects have become an increasing problem growing from both human and natural influences. Pace and Cole et al. (1999) suggest that these cascades are less likely in diverse food webs with a strong presence of omnivory. We have already mentioned that IGP is a specialized form of omnivory, and it should also work to prevent drastic, irreversible phase shifts in the environment.

IGP also has the ability to suppress the impacts of trophic cascades that often lead to prey suppression and ultimately release species of the next lower trophic level from high levels of predation. Finke and Denno (2005) found that increasing the proportion of intraguild predators among the general predator population will dampen the cascading predator effects on lower trophic levels. Intraguild predators interact conflictly, resulting in reduced predation on a shared prey or herbivore population. Fortunately, the cascade is dampened enough to avoid extreme decrease in plant production and biomass that should follow decreased herbivore suppression (Finke and Denno 2005). Since IGP occurs frequently in nature, it is likely to be a common mediator of many trophic cascades.

Functional Response

We will use the equations (2.2) from Holt and Polis (1997) as the basis for our model derivations. Their major assumptions were that the plant, P , grows according to the logistic model in the absence of predators and that each consumer follows a linear functional response (type I). If we want to truly model realistic conditions then we will have to include

a more complicated functional response.

The idea of functional response was introduced as the change in consumption of prey as a response of changes in prey densities by the predator (Solomon 1949) and was expanded to include three types of functional response by Holling (1959). Holling (1959) realized that there are certain time consuming components that must be incorporated into a predator's response. Type I functional response is the simplest expression of the relationship between time and predation rate:

$$p = cN_{prey}T_s \quad (2.7)$$

where p is the predation rate on N_{prey} during a given search time, T_s , and c is a constant equal to the searching rate multiplied by the probability of finding prey (Holling 1959). The only time consuming part of this type of functional response is the time needed for searching. By using $a = cT_s$ then a type I functional response will resemble the following in our models:

$$p = aN_{prey} \quad (2.8)$$

Next, Holling (1959) derives type II functional response that includes both searching time, already noted as T_s and handling time, T_h . Then the total time needed is T where:

$$T = T_s + T_h p \quad (2.9)$$

This can be rewritten as:

$$T_s = T - T_h p \quad (2.10)$$

Then equation (2.7) can be rewritten to include handling time with respect to the total number of prey eaten:

$$\begin{aligned} p &= cN_{prey}(T - T_h p) \\ p &= \frac{cN_{prey}T}{1 + cN_{prey}T_h} \end{aligned} \quad (2.11)$$

This equation gives us the recognizable decreasing consumption rate. As the number of prey increases so does the predation rate, and more time is spent handling prey than

searching for prey. However, at extremely high prey densities, predation rates begin to plateau when saturation is reached. Predators can only eat so much. If we use $a = cT_s$ and $b = cT_h$, then a type II functional response can be rewritten as:

$$p = \frac{aN_{prey}}{1 + bN_{prey}} \quad (2.12)$$

The signature sigmoid curve of a type III functional response occurs because of more complicated dynamics and time consuming function. Here we can include identification time, resting time, learning time, etc. Predators may also switch to consuming more abundant prey. The ability of prey to seek cover and refuge also adds to total consumption time. At high densities it is similar to type II functional response in that saturation occurs and predation rate levels off. However, prey consumption is low at low densities and increases as a sigmoidal curve. Following from equation (2.12), an equation for type III functional response can be written as:

$$p = \frac{aN_{prey}^2}{1 + bN_{prey}^2} \quad (2.13)$$

Figure (2.3) shows us the traditional functional response curves in terms of increasing prey densities.

Using equations (2.2), we develop a general three-species IGP model using functional response:

$$\begin{aligned} \frac{dP}{dt} &= P \left[r \left(1 - \frac{P}{K} \right) - f(P)M - g(P)G \right] \\ \frac{dG}{dt} &= G [b_g g(P)P - h(G)M - d_g] \\ \frac{dM}{dt} &= M [b_m f(P)P + \beta h(G)G - d_m] \end{aligned} \quad (2.14)$$

where $f(P)$, $g(P)$, and $h(G)$ are the functional responses of IG predator to shared prey, IG prey to shared prey, and IG predator to IG prey respectively. If we consider the IG predator to be a generalist predator rather than a specialist then we have:

$$\begin{aligned} \frac{dP}{dt} &= P \left[r_P \left(1 - \frac{P}{K_P} \right) - f(P)M - g(P)G \right] \\ \frac{dG}{dt} &= G [b_g g(P)P - h(G)M - d_g] \\ \frac{dM}{dt} &= M \left[r_m \left(1 - \frac{M}{K_m} \right) + b_m f(P)P + \beta h(G)G \right] \end{aligned} \quad (2.15)$$

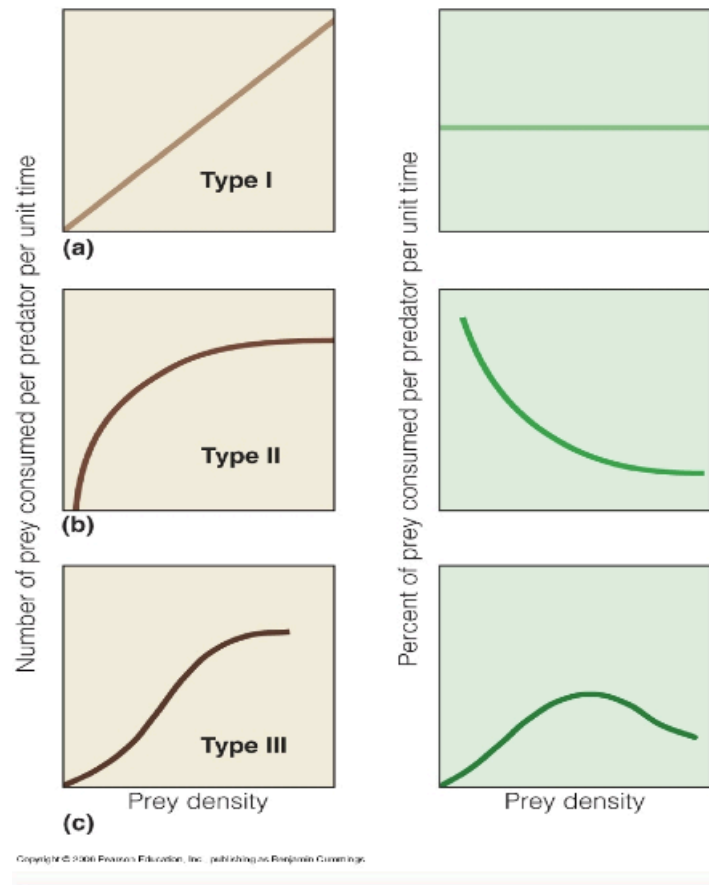


Figure 2.3: (a) type I, linear response; (b) type II, concave response; (c) type III, sigmoid response (Copyright 2006 Pearson Education, Inc., publishing as Benjamin Cummings)

where K_i and r_i are the carrying capacity and growth rate of species i .

We base our model derivations on these explanations of functional response and systems (2.14) and (2.15). A basic linear response can describe the relationship between the basal resource and IG prey or IG predator because searching time is the only factor contributing to time consumption. Handling time is negligible because there is no struggle while consuming resources. Then we have a more complicated relationship between IG predator and IG prey. We use the results from Schaubert et al. (2004) to determine the functional response of G to changes in densities of M . They conducted field experiments to determine the functional response of the white-footed mouse to gypsy moth pupae. If we similarly assume IG prey to be an insect with the same life-stages and an IG predator that feeds on pupae, then we can use their results to identify the appropriate functional

response. They found that an accelerating functional response (type III) is more appropriate than a decelerating one (type II) because of the positive relationship between daily predation rate on pupae and pupal density. They conclude that an even more complicated type III response is necessary to prevent prey extinction and thus promote coexistence (Schauber et al. 2004).

The differences in dynamics between generalist and specialist predators could be important to the role of IGP in biological control and conservation. So we will consider continuous models where IG predator, M , is a generalist vs. a specialist to compare conditions for persistence, equilibrium, etc. We will also derive a model involving discrete dynamics to see if simulations suggests differences in dynamics for the same system. Hastings (1983) studied the equilibrium of a system that relied heavily on juvenile populations because only juveniles were subject to predation. Thus, the length of the vulnerable juvenile period was critical to the local stability of equilibrium. In circumstances such as this, it is important to incorporate differences in age-structure into analyses. This can be done by using a semi-discrete time series model where dynamics vary based on the age-structure (stage-structure life cycle) of our IG prey, an insect.

2.3 Model Derivations

We consider a specific case where three species are involved in stage-structured, asymmetric IGP. Asymmetric IGP occurs when one species, the IG predator, is always the predator and the second, the IG prey, is always the prey (Polis et al. 1989). Stage, or age, structured IGP considers the differences in dynamics between stages. For instance, a predator may feed on only one stage of its prey. These differences are often dependent on species size during certain stages and time of year that predation is occurring. Figure 2.4 shows an asymmetric, stage-structured, IGP system where P , the shared prey, represents a primary producer, M , the IG prey, represents an herbivore, and G , the IG predator, represents a predator. The predator feeds on the seeds of the plant and adult herbivores. Additionally, pupae of the herbivore feed on the leaves of the plant.

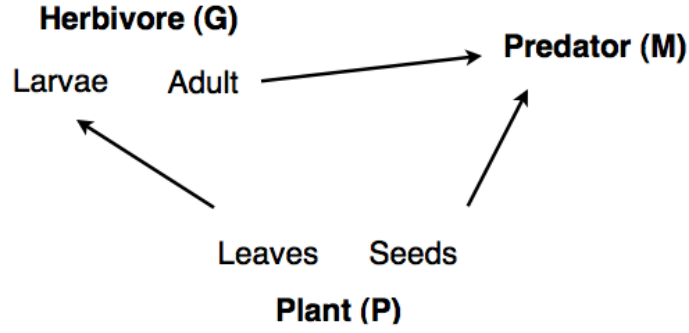


Figure 2.4: Stage-structured, asymmetric IGP diagram where the herbivore (G) is the equivalent of the IG prey. The predator (M) is the equivalent of the IG predator. The plant (P) is the equivalent of the shared prey. The herbivore and predator feed on different growth stages of the plant. Pupae of the herbivore feed on the plant, while adult herbivores are involved with predation by the predator.

The most frequently used methods to model food web dynamics involve either discrete or continuous time-series. A third, less known method uses a semi-discrete time series where dynamics are separated by both stage-structures and time (Singh and Nisbet 2007). We can walk through the model derivations for each of the three separate time series. While each of them adhere as closely as possible to similar assumptions, we hypothesize that dynamics will vary significantly between models.

Continuous Model

A continuous time-series model is useful when considering overlapping generations. It allows us to look at the rate of change of populations over time. Let $P(t), G(t), M(t)$ be the population biomass of plant (shared prey), consumer (IG prey) and predator (IG predator) respectively at time t . For purpose of analyses we will consider separate models for specialist and generalist predators. Suppose that species P, G, M satisfy the following ecological assumptions:

- In the absence of predator species G and M , plant species P follows a logistic growth function.
- In the absence of both P and G , generalist predator M will persist independently following a logistic growth function.

- Specialist predator M feeds relies on only P and G for survival.
- In the absence of both P and G , specialist predator M cannot exist.
- Predator M feeds on both P and G , but herbivore G only feeds on P .
- G feeds on P following a Holling type I functional response because searching time is the only factor of time consumption that will limit the predation rate. Handling time and other more complicated dynamics are not applicable. (Holling 1959)
- M feeds on P following a Holling type I functional response for the same reason.
- G is an insect and M feeds on G following a Holling type III functional response following experiments done by Schaubert et al. (2004) who found a positive relationship between predation rate and pupae densities, causing an accelerating response.

Parameters	Biological Meanings
r_p	maximum growth rate of resource
r_m	maximum growth rate of IG predator
K_p	carrying capacity of resource
K_m	carrying capacity of IG predator
a_g	predation rate of IG prey for resource
a_m	predation rate of IG predator for resource
a	maximum population of IG prey killed by IG predator
b	IG prey density at which the population killed by IG predator reached half of its maximum
e_g	bio-mass conversion rate from resource to IG prey
e_m	bio-mass conversation rate from IG prey to IG predator
d_g	the mortality rate of IG prey
d_m	the mortality rate of IG predator

Table 2.1: Parameters Table

Then based on the assumptions above, a continuous time IGP model with specialist predator can be described as follows:

$$\begin{aligned}
\frac{dP}{dt} &= P \left[r_p \left(1 - \frac{P}{K_p} \right) - a_g G - a_m M \right] \\
\frac{dG}{dt} &= G \left[e_g a_g P - \frac{aMG}{G^2 + b^2} - d_g \right] \\
\frac{dM}{dt} &= M \left[e_m a_m P + \frac{e_m a G^2}{G^2 + b^2} - d_m \right]
\end{aligned} \tag{2.16}$$

while a continuous time IGP model with generalist predator can be described as follows:

$$\begin{aligned}
\frac{dP}{dt} &= P \left[r_p \left(1 - \frac{P}{K_p} \right) - a_g G - a_m M \right] \\
\frac{dG}{dt} &= G \left[e_g a_g P - \frac{aMG}{G^2 + b^2} - d_g \right] \\
\frac{dM}{dt} &= M \left[r_m \left(1 - \frac{M}{K_m} \right) + e_m a_m P + \frac{e_m a G^2}{G^2 + b^2} \right]
\end{aligned} \tag{2.17}$$

Parameters values are assigned according to biological meanings in Table 1. K_i and r_i assign a carrying capacity and growth to species i when considering a logistic growth rate. a_i is used as a searching rate of species i for the plant, and e_i is the conversion efficiency of biomass between trophic levels from plant to species i . The searching rate decreases the amount of attainable biomass for consumption. Furthermore, the amount of biomass transferred from one trophic level to another decreases drastically between species. Parameters a and b describe the type III functional response between M and G .

Discrete Model

A discrete time-series model is most useful when dealing with non-overlapping generations. Let P_t , G_t , and M_t be the population biomass of plant, herbivore, and predator at season t . Then P_{t+1} , G_{t+1} , and M_{t+1} will be the population biomass of plant, herbivore, and predator at season $t + 1$ where 1 is equivalent to one year and one full generation of the insect. Suppose that species P , G , and M satisfy the following ecological assumptions:

- In the absence of species G and M , plant species P follows Ricker's model:

$$N_{t+1} = N_t e^{r(1 - \frac{N_t}{K})} \tag{2.18}$$

where N_t is the population biomass density at generation t and N_{t+1} is the population biomass density at generation $t + 1$.

- Four distinct stages are included 1) P grows independently of the M and G , 2) G attacks P , 3) M attacks G , and 4) M also attacks P .
- Both G and M search for plants randomly.

- The predation rate of predator M on herbivore G follows a Holling Type III functional response.
- Generalist predator M grows independently of G and P , but specialist predator M relies on solely G and P for survival.

Then a discrete time IGP model with specialist predator can be described as follows:

$$\begin{aligned}
P_{t+1} &= P_t e^{(r_p \left(1 - \frac{P_t}{K_p}\right) - a_g G_t - a_m M_t)} \\
G_{t+1} &= e_g P_t e^{r_p \left(1 - \frac{P_t}{K_p} - \frac{a M_t G_t}{G_t^2 + b^2}\right)} [1 - e^{-a_g G_t}] \\
M_{t+1} &= e_m e_g P_t e^{r_p \left(1 - \frac{P_t}{K_p}\right)} [1 - e^{-a_g G_t}] \left[1 - e^{-\frac{a M_t G_t}{G_t^2 + b^2}}\right]
\end{aligned} \tag{2.19}$$

while a discrete time IGP model with generalist predator can be described as follows:

$$\begin{aligned}
P_{t+1} &= P_t e^{(r_p \left(1 - \frac{P_t}{K_p}\right) - a_g G_t - a_m M_t)} \\
G_{t+1} &= e_g P_t e^{r_p \left(1 - \frac{P_t}{K_p} - \frac{a M_t G_t}{G_t^2 + b^2}\right)} [1 - e^{-a_g G_t}] \\
M_{t+1} &= M_t e^{r_m \left(1 - \frac{P_t}{K_m}\right) + e_m e_g P_t e^{r_p \left(1 - \frac{P_t}{K_p}\right)} [1 - e^{-a_g G_t}] \left[1 - e^{-\frac{a M_t G_t}{G_t^2 + b^2}}\right]}
\end{aligned} \tag{2.20}$$

where the biological meanings of parameters can be found in Table 2.1.

An alternative discrete time model can be derived based on our continuous time series models (2.16) and (2.17). Then a second discrete time IGP model with a specialist predator can be described as follows:

$$\begin{aligned}
P_{t+1} &= P_t e^{(r_p \left(1 - \frac{P_t}{K_p}\right) - a_g G_t - a_m M_t)} \\
G_{t+1} &= G_t e^{(e_g a_g P_t - \frac{a M_t G_t}{G_t^2 + b^2} - d_g)} \\
M_{t+1} &= M_t e^{(e_m a_m P_t + \frac{e_m a G_t^2}{G_t^2 + b^2} - d_m)}
\end{aligned} \tag{2.21}$$

while a second discrete time IGP model with generalist predator can be described as follows:

$$\begin{aligned}
P_{t+1} &= P_t e^{(r_p \left(1 - \frac{P_t}{K_p}\right) - a_g G_t - a_m M_t)} \\
G_{t+1} &= G_t e^{(e_g a_g P_t - \frac{a M_t G_t}{G_t^2 + b^2} - d_g)} \\
M_{t+1} &= M_t e^{(r_m \left(1 - \frac{M_t}{K_m}\right) + e_m a_m P_t + \frac{e_m a G_t^2}{G_t^2 + b^2})}
\end{aligned} \tag{2.22}$$

Semi-discrete time-series models are typically the most realistic way of modeling food web dynamics. It takes the differences in dynamics between stage-structures into consideration. The most important state-structures to consider here are those of the herbivore, an insect. Since the life-cycle of a typical insect occurs over a single year, we can divide a year into seasons (Figure 2.5). Seasonal dynamics will be modeled with continuous, differential equations while dynamics in between seasons will mimic a discrete time-series.

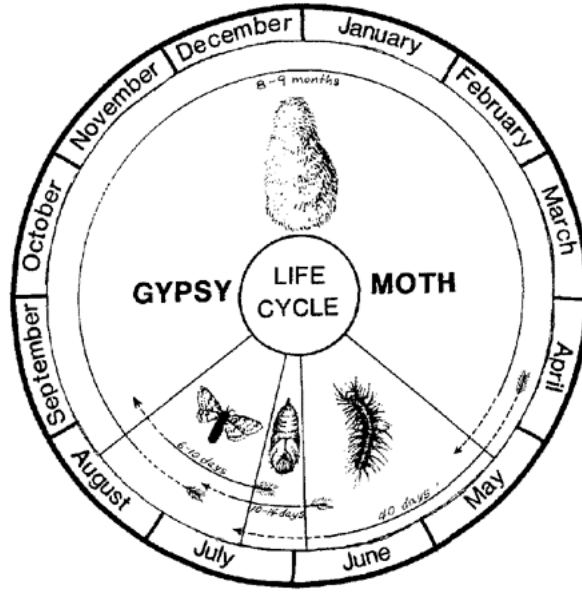


Figure 2.5: Stage-structured life cycle of insect (Grupp 2012)

We divide one year from the season t to the $t + 1$ into four sub-time intervals as $[t, t + t_{sp}]$, $[t + t_{sp}, t + t_{sp} + t_{su}]$, $[t + t_{sp} + t_{su}, t + t_{sp} + t_{su} + t_f]$ and $[t + t_{sp} + t_{su} + t_f, t + 1]$ where the length of four seasons in a year are spring (t_{sp}), summer (t_{su}), fall (t_f) and winter ($1 - t_{sp} - t_{su} - t_f$). The four seasons correspond to the four stages in the life cycle of an insect: egg (spring), larvae (summer), pupae (fall), and adult (winter). Additional parameters from Table 2 are needed to designate discrete time-series changes in between seasons. s_i , survival rate, is used to include changes in species i between seasons. q is the storage ratio of P through the winter.

Consider the following assumptions:

Parameters	Biological Meanings
d_{g2}	external mortality rate of IG prey in the summer
d_{g3}	external mortality rate of IG prey in the fall
s_g	survival rate of IG prey in egg form
s_p	survival ratio of resource over the winter
q	storage ratio of resource biomass

Table 2.2: Additional Parameters

- Seasons active: P are active the whole year. G are active only in the summer. M are active only in the fall and winter.
- In the absence of the M and G , P follows a logistic growth function.
- M is a generalist predator and follows a logistic growth function In the absence of the G and P .
- G searches for leaves of P randomly in the summer, $[t + t_{sp}, t + t_{sp} + t_{su}]$. They then become pupae and eventually adults during the fall, $[t + t_{sp} + t_{su}, t + t_{su} + t_f]$. They remain in egg form throughout the winter, $[t + t_{sp} + t_{su} + t_f, t + 1]$.
- The nutrients in M comes from three parts: 1) predation on pupae of G following a Holling-type III functional response during fall, $[t + t_{sp} + t_{su}, t + t_{sp} + t_{su} + t_f]$, 2) feeding on seeds of P following a Holling-type I functional response during winter, $[t + t_{sp} + t_{su} + t_f, t + 1]$, and 3) outside resources.

Consider $P(\tau), G(\tau), M(\tau)$ to be the biomass of plant, herbivore and predator at time τ , then we use semi-discrete methods (Singh and Nisbet 2007) to derive the model in detail as follows:

• **Spring:**

$$\begin{aligned}
\frac{dP(\tau)}{d\tau} &= r_p P \left[1 - \frac{P}{K_p}\right] \\
\frac{dM(\tau)}{d\tau} &= r_m M \left[1 - \frac{M}{K_m}\right] \\
\tau &\in [0, t_{sp}], P(0) = (1 - q)P_t + s_p q P_t e^{-a_m M_t (t_{sp} + t_{su} + t_f)}, M(0) = M_t
\end{aligned} \tag{2.23}$$

The output of (2.23) is

$$P_t(t_{sp}) = P(t_{sp}), M_t(t_{sp}) = M(t_{sp}).$$

• **Summer:**

$$\begin{aligned}\frac{dP(\tau)}{d\tau} &= r_p P \left[1 - \frac{P}{K_p} \right] - a_g P G \\ \frac{dG(\tau)}{d\tau} &= G [e_g a_g P - d_{g2}] \\ \frac{dM(\tau)}{d\tau} &= r_m M \left[1 - \frac{M}{K_m} \right] \\ \tau &\in [0, t_{su}], P(0) = P_t(t_{sp}), G(0) = s_g G_{t-1}(1), M(0) = M_t(t_{sp})\end{aligned}\tag{2.24}$$

The output of (2.24) is

$$P_t(t_{sp} + t_{su}) = P(t_{su}), G_t(t_{sp} + t_{su}) = G(t_{su}), M_t(t_{sp} + t_{su}) = M(t_{su}).$$

• **Fall:**

$$\begin{aligned}\frac{dP(\tau)}{d\tau} &= r_p P \left[1 - \frac{P}{K_p} \right] \\ \frac{dG(\tau)}{d\tau} &= -d_{g3} G - \frac{aG^2 M}{G^2 + b^2} \\ \frac{dM(\tau)}{d\tau} &= r_m M \left[1 - \frac{M}{K_m} \right] + \frac{ae_m G^2 M}{G^2 + b^2} \\ \tau &\in [0, t_f], P(0) = P_t(t_{sp} + t_{su}), G(0) = G_t(t_{sp} + t_{su}), M(0) = M_t(t_{sp} + t_{su})\end{aligned}\tag{2.25}$$

The output of (2.25) is

$$P_t(1) = P(t_f), G_t(t_{sp} + t_{su} + t_f) = G(t_f), M_t(t_{sp} + t_{su} + t_f) = M(t_f).$$

• **Winter:**

$$\begin{aligned}P_{t+1} &= P_t(1) \\ G_{t+1} &= G_t(1) = s_g G_t(t_{sp} + t_{su} + t_f) \\ M_{t+1} &= M_t(1) = M_t(t_{sp} + t_{su} + t_f) + qP_{t+1} [1 - e^{-a_m M_t(t_{sp} + t_{su} + t_f)}]\end{aligned}\tag{2.26}$$

where spring follows from the outputs of winter.

Gypsy moth, White-footed mouse, and Oak

Gypsy moths, white-footed mice, and oak trees are involved in a specific case of IGP that mimics these dynamics. Oaks (*Quercus* spp.) are deciduous hardwoods that produce the

main diet of the white-footed mouse, acorns. Mast seeding, the intermittent production of large seed crops in the fall, can drive large fluctuations in abundance of granivores, and it may have indirect effects that extend to a surprising array of species and ecological processes. Acorn mast seeding has been hypothesized to indirectly ignite gypsy moth outbreaks that are mediated by the direct effect of acorns on the abundance of white-footed mice (Elkinton et al. 1998). Experimental removal of white-footed mice has suggested that moth outbreaks are correlated with reduced mouse density (Jones et al. 1998). This is an indirect effect of low acorn production.

Lymantria dispar, the gypsy moth, is annually responsible for millions of acres of defoliation in the Northeastern United States. Even though the species has more than 250 known host plants, it consistently prefers oak. The life cycle of gypsy moths involves four stages: eggs, larvae, pupae, and adult moths. Gypsy moths go through an entire life cycle in one year, and larvae first begin to appear around the same time that leaves emerge in the late spring or early summer. Thus, only larvae damage vegetation. Mature caterpillars pupate from mid-June through early July. The white-footed mouse (*Peromyscus leucopus*) feeds on pupae, and it is an important regulator of gypsy moth in this stage. More recent studies in northeastern United States have reaffirmed the white-footed mouse as the most important predator of endemic populations of gypsy moths (Hastings et al. 2002).

Gypsy moth populations often experience extreme episodic outbreaks. However, they also remain at relatively low density for long intervals of time. Previous studies have analyzed why gypsy moth populations are maintained at low density some years but are able to erupt into outbreaks other years (Jones et al. 1998, Elkinton et al. 1998). The white-footed mouse is a principle predator of the gypsy moth, and changes in population density of both species are correlated with each other. Additionally, increases in mouse abundance have been associated with large acorn crops from oak trees in the previous mast season (Elkinton et al. 1996). Since the leaves of the oak tree also act as a principle resource for gypsy moths (Elkinton et al. 1996), the interactions between gypsy moths, white-footed mice, and oak trees in the Northeastern United States can be described using

a similar IGP model to those described. Mice and moths are in competition for a single resource, oak trees. However, they also experience predator/prey relationships where a larger, white-footed mouse, feeds on a smaller prey, gypsy moths. Stage-structure also plays an important role when adult mice feed on gypsy moth pupae and acorns, and adult gypsy moths feed on the leaves of oak trees. The relationship is asymmetric because the IG predator, white-footed mouse, feeds on the IG prey, gypsy moth, but not the other way around. A semi-discrete model, similar to the one discussed, would be most helpful in describing the mechanisms of this system: oak (P), gypsy moth (G), and white-footed mouse (M). Ecologists will be able to study how the white-footed mouse regulates the dynamics of gypsy moths and how acorn production indirectly affects gypsy moth outbreaks.

MODEL ANALYSES

Mathematical analysis can prove extremely beneficial in conservation and management efforts. Dating back to some of the first predator-prey population models, analyses and simulations have been used to predict behavior and the likelihood for species persistence. The same methods used for stability and equilibria analysis of the two-species Lotka-Volterra predator-prey model may be applied our three-species intraguild predation model. When dealing with more complicated models, especially those that are not limited to type I functional response, rescaling can be used to minimize parameters. From here, data from analyses is used to perform realistic computer simulations. Simulations allow us to modify different parameter values to see what effects they have on dynamics. We can also compare the dynamics of different models, i.e. IGP with a generalist vs. specialist predator or continuous vs. discrete time-series. The most realistic model that we have derived the the semi-discrete time-series model. A more complicated model significantly complicates the potential for analyses, but model simulations can still be run to aid in future research. Here, we begin by walking through a typical model analysis using the Lotka-Volterra predator-prey model.

3.1 Lotka-Volterra Stability and Equilibria Analysis

We used the traditional two-species Lotka-Volterra model for predator-prey relationships as the point of departure for our model derivations. Thus, it seems appropriate that we use it here as an introduction to model dynamics. Recall the equations for a two-species system:

$$\begin{aligned}\frac{dN_1}{dt} &= rN_1 - pN_1N_2 \\ \frac{dN_2}{dt} &= cpN_1N_2 - dN_2\end{aligned}\tag{3.1}$$

where N_1 and N_2 are the population biomass densities of prey and predator respectively. Note that r is the per capita growth rate of the prey independent of the predator. Then p is

the predation rate, c is the conversion rate of consumed prey to new predators, and d is the external mortality rate of the predator.

The dynamics of this system are relatively well-known and used as the basis for analyses of population dynamics. We will show here that a stable equilibrium point does not exist and that the predator and prey populations are stuck in an endless cycle of fluctuations, see Figure (3.1). Perhaps the most famous case of this cyclic pattern found in nature is the lynx/hare predator-prey relationship (Elton and Nicholson 1942). Unfortunately, this

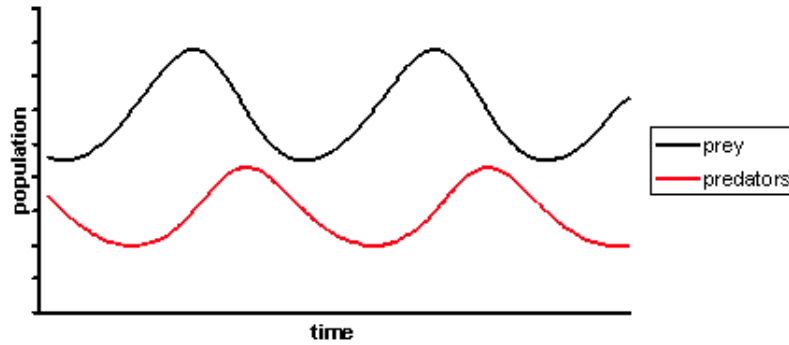


Figure 3.1: Oscillatory predator-prey relationship.

pattern is not as common as one would suspect. In fact, it is fairly rare, implying that additional specific factors must be added to accurately model any predator-prey interaction that occurs in nature. None the less, it is easy to look at equations (3.1) to figure out what is causing these fluctuations. Since the prey population grows exponentially in the absence of predators, we know the the prey has no trouble finding food at all times. The population size of the predator is entirely determined by the population size of its prey. When the prey population grows, the predation rate increases causing prey populations to decline. This subsequently causes predator populations to decline because of the lack of food. Then the prey population has a chance to grow once again because of a subsequently low predation rate. This pattern will continue unless outside factors cause a shift in dynamics.

An equilibrium point is one where the growth rates of all populations are equal to 0. If we do this for equations (3.1) then we get $N_1 = \frac{d}{cp}$ and $N_2 = \frac{r}{p}$. We also have

$N_1 = 0$ and $N_2 = 0$. What we essentially just found was the isoclines for species N_1 and N_2 , lines that connect points where there is zero growth rate. For more complicated systems, especially those containing more than two species, this is easily done using computer programs such as Maple. Prey population densities greater than $\frac{d}{cp}$ will result in increasing prey densities while densities less than $\frac{d}{cp}$ will result in decreasing densities. Almost the same can be said for predators. Densities greater than $\frac{r}{p}$ will decrease, and densities less than $\frac{r}{p}$ will increase. If we combine these onto the same graph then we get something that looks like Figure (3.2). If we follow the pattern around in a counter-clockwise direction,

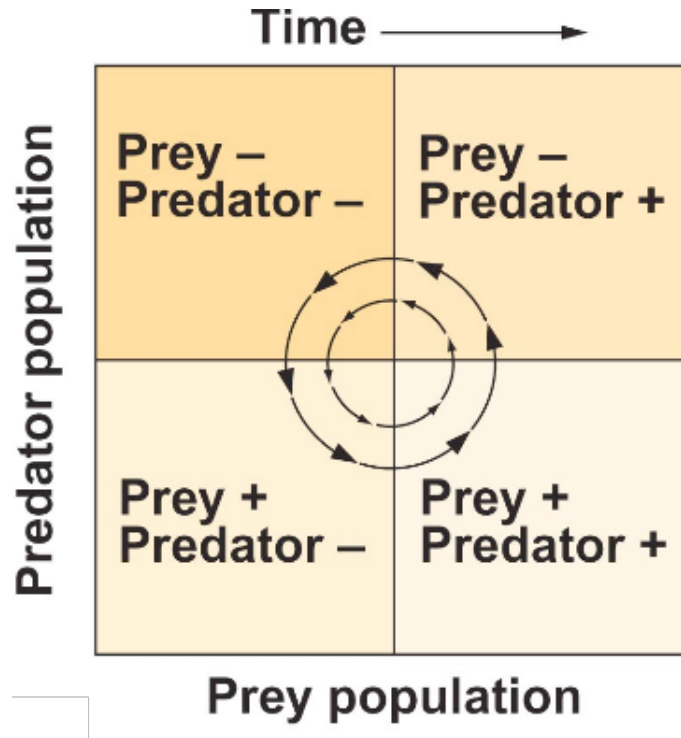


Figure 3.2: Lotka-Volterra predator-prey isoclines. The vertical line represents $N_1 = \frac{d}{cp}$ and the horizontal line represents $N_2 = \frac{r}{p}$. They cross in the middle where there is zero growth rate for both prey and predator populations. + indicates a growing population density and - represents a declining population density. The cyclic pattern flows counter-clockwise. (Copyright 2006 Pearson Education, Inc., publishing as Benjamin Cummings)

we notice the cyclic dynamics that were previously described. A growing prey population and declining predator population (bottom left) will eventually cause an increasing predator population due to an increased predation rate (bottom right). A surplus of predators will then limit prey population growth to the point where it begins to decline (top right).

Without food, predators cannot live and begin to die out (top left).

From here, we need to create a Jacobian matrix with the partial derivative of equations (3.1) with respect to N_1 and N_2 (Stevens 2009). We use the partial derivative because we want to know the changes in population densities in response to changes of each population separately:

$$\begin{pmatrix} \frac{\partial \frac{dN_1}{dt}}{\partial N_1} & \frac{\partial \frac{dN_1}{dt}}{\partial N_2} \\ \frac{\partial \frac{dN_2}{dt}}{\partial N_1} & \frac{\partial \frac{dN_2}{dt}}{\partial N_2} \end{pmatrix}$$

If we use $N_1^* = \frac{dN_1}{dt}$ and $N_2^* = \frac{dN_2}{dt}$ then our matrix looks simpler:

$$\begin{pmatrix} \frac{\partial N_1^*}{\partial N_1} & \frac{\partial N_1^*}{\partial N_2} \\ \frac{\partial N_2^*}{\partial N_1} & \frac{\partial N_2^*}{\partial N_2} \end{pmatrix}$$

When we substitute in our partial derivatives we get:

$$\begin{pmatrix} r - pN_2 & -pN_1 \\ cpN_2 & cpN_1 - d \end{pmatrix}$$

Next, we can replace N_1 and N_2 in our Jacobian matrix with the equilibria that we found by setting the population growth rates equal to zero. In this case, we have two equilibria. For the first, $N_1 = 0$ and $N_2 = 2$, our new matrix looks like:

$$\begin{pmatrix} r & 0 \\ 0 & -d \end{pmatrix}$$

Since predator-prey equations are typically more complex than this, we use Maple to find the eigenvalues of our matrix. Eigenvalues for the first equilibrium are r and $-d$. Since r is always positive, this is an unstable equilibrium point which means that both species will not remain stable at extinction. This makes sense because the prey population grows exponentially in the absence of the predator.

Next, replace N_1 and N_2 with $N_1 = \frac{d}{cp}$ and $N_2 = \frac{r}{p}$ in the Jacobian matrix:

$$\begin{pmatrix} 0 & -\frac{d}{c} \\ rc & 0 \end{pmatrix}$$

where two imaginary eigenvalues suggest that populations will oscillate. This is precisely what we expected to see.

Eigenanalysis

The use of eigenvalues is critical in the analysis of population growth models. Thus, it is worth taking the time to discuss how they are used. Stability theory addresses the trajectories of systems after small perturbations of initial conditions. As we just saw, eigenvalues are commonly used to determine the stability of equilibria points. The use of eigenvalues to determine stability is based on theory by Lyapunov (Khalil 1996) where eigenvalues characterize the behavior of nearby points in an n -dimensional phase space. A phase space is identified as a space where all possible states of a system are represented as plotted points over time. The phase space ultimately represents all that a system can be, and its shape can identify dynamics that may not be otherwise obvious. For example, trajectories of a phase plane may represent a limit cycle if an orbit eventually approaches a repeating cycle without being attracted or repelled from the pattern. An attracting fixed point will occur when trajectories approach a single point in the phase space. If trajectories appear to move away from this point, then the system is unstable.

The signs of eigenvalues are most important when determining stability because they determine the direction that a trajectory will follow in a phase space. Figure 3.3 summarizes the behavior of trajectories within a 2-dimensional phase space (phase plane) where arrows indicate the movement of a system.

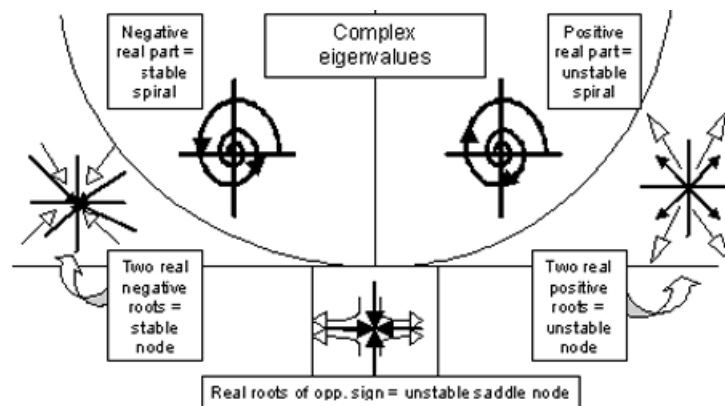


Figure 3.3: Behavior of a trajectory within a phase plane depending on the eigenvalue calculated.

Negative eigenvalues suggest that a trajectory will be attracted as a dampening orbit to an attracting fixed point. Thus, in order for a fixed point to be stable all eigenvalues must be negative (Stevens 2009). If all three are positive then the equilibrium point is unstable and nearby trajectories will be driven away from the fixed point. If there is at least one positive eigenvalue then there is a saddle point that is generally unstable. It is also possible for eigenvalues to be complex numbers. When the real part of a complex eigenvalue is positive then nearby trajectories oscillate away from the steady-state value with an increasing amplitude. Consequently, when the real part is negative then oscillations decrease in amplitude. We cannot forget the situations when the real part is equal to zero. This causes an oscillation around the steady-state values with a constant amplitude. In other words, it causes a cyclic pattern like the one we saw with the two-species Lotka-Volterra predator-prey model. Finally, all eigenvalues could be equal to zero. When this happens, the system remains at the position to which it was disturbed. We will refer to these conditions in the analysis that follows.

3.2 Mathematical Analysis - Continuous

Recall the equations for three-species intraguild predation (IGP) from Chapter 2. Parameters and their biological meanings are listed in Table (3.1). The continuous time IGP model with specialist predator is described by:

$$\begin{aligned}\frac{dP}{dt} &= P \left[r_p \left(1 - \frac{P}{K_p} \right) - a_g G - a_m M \right] \\ \frac{dG}{dt} &= G \left[e_g a_g P - \frac{aMG}{G^2 + b^2} - d_g \right] \\ \frac{dM}{dt} &= M \left[e_m a_m P + \frac{e_m aG^2}{G^2 + b^2} - d_m \right]\end{aligned}\tag{3.2}$$

while a continuous time IGP model with generalist predator can be described as follows:

$$\begin{aligned}\frac{dP}{dt} &= P \left[r_p \left(1 - \frac{P}{K_p} \right) - a_g G - a_m M \right] \\ \frac{dG}{dt} &= G \left[e_g a_g P - \frac{aMG}{G^2 + b^2} - d_g \right] \\ \frac{dM}{dt} &= M \left[r_m \left(1 - \frac{M}{K_m} \right) + e_m a_m P + \frac{e_m aG^2}{G^2 + b^2} \right]\end{aligned}\tag{3.3}$$

Parameters	Biological Meanings
r_p	maximum growth rate of resource
r_m	maximum growth rate of IG predator
K_p	carrying capacity of resource
K_m	carrying capacity of IG predator
a_g	predation rate of IG prey for resource
a_m	predation rate of IG predator for resource
a	maximum population of IG prey killed by IG predator
b	IG prey density at which the population killed by IG predator reached half of its maximum
e_g	bio-mass conversion rate from resource to IG prey
e_m	bio-mass conversation rate from IG prey to IG predator
d_g	the mortality rate of IG prey
d_m	the mortality rate of IG predator

Table 3.1: Parameters Table of System (3.4) and (3.5)

Assume that all parameters are strictly positive, then for the convenience of mathematical analysis, we can simplify System 3.2 as 3.4 by letting

$$x = \frac{P}{K_p}, y = \frac{a_g G}{r_p}, z = \frac{a_m M}{r_p}, \tau = r_p t, \gamma_1 = \frac{e_g a_g K_p}{r_p}, a_1 = \frac{a_m a}{e_g K_p},$$

and

$$\beta = \frac{r_p b}{a_g}, d_1 = \frac{d_g}{e_g a_g K_p}, \gamma_2 = \frac{e_m a_m K_p}{r_p}, a_2 = \frac{a}{a_m K_p}, d_2 = \frac{d_m}{e_m a_m K_p}.$$

$$\begin{aligned} x' &= x(1 - x - y - z) \\ y' &= \gamma_1 y \left(x - \frac{a_1 y z}{y^2 + \beta^2} - d_1 \right) \\ z' &= \gamma_2 z \left(x + \frac{a_2 y^2}{y^2 + \beta^2} - d_2 \right). \end{aligned} \tag{3.4}$$

Similarly, System 3.3 can be rewritten as 3.5 by letting

$$x = \frac{P}{K_p}, y = \frac{a_g G}{r_p}, z = \frac{a_m M}{r_p}, \tau = r_p t, \gamma_1 = \frac{e_g a_g K_p}{r_p}, a_1 = \frac{a_m a}{e_g K_p}, \beta = \frac{r_p b}{a_g},$$

and

$$d_1 = \frac{d_g}{e_g a_g K_p}, \gamma_2 = \frac{e_m a_m K_p}{r_p}, a_2 = \frac{a}{a_m K_p}, a_3 = \frac{r_m}{e_m a_m K_p}, a_4 = \frac{r_p r_m}{K_m a_m^2 e_m K_p}, d_2 = \frac{d_m}{e_m a_m K_p}.$$

$$\begin{aligned} x' &= x(1 - x - y - z) \\ y' &= \gamma_1 y \left(x - \frac{a_1 y z}{y^2 + \beta^2} - d_1 \right) \\ z' &= \gamma_2 z \left(a_3 - a_4 z + x + \frac{a_2 y^2}{y^2 + \beta^2} \right). \end{aligned} \tag{3.5}$$

Rescaling helps to minimize parameters and facilitate analyses. Before continuing, it is necessary to point out that both systems (3.4) and (3.5) are positively invariant and bounded in \mathbf{R}^3 (Kang and Wedekin 2012). In other words, once a trajectory enters the limits of either system, it does not leave. Furthermore, all conditions for species persistence and extinction occur in \mathbf{R}^3 .

We also know that x and z are further bounded by the following conditions (Kang and Wedekin 2012):

$$\limsup_{\tau \rightarrow \infty} x(\tau) \leq 1 \text{ and } \frac{a_3}{a_4} \leq \liminf_{\tau \rightarrow \infty} z(\tau) \leq \limsup_{\tau \rightarrow \infty} z(\tau) \leq \frac{1 + a_2 + a_3}{a_4}.$$

which most importantly says that z is persistent in System (3.5).

Boundary Equilibria and Their Stability

It is easy to check that System (3.4) has the following boundary equilibria if $d_i < 1, i = 1, 2$:

$$(0, 0, 0), (1, 0, 0), (d_1, 1 - d_1, 0), \text{ and } (d_2, 0, 1 - d_2)$$

while System (3.5) has the following boundary equilibria if $d_1 < 1$ and $\frac{a_3}{a_4} < 1$:

$$(0, 0, 0), (1, 0, 0), (d_1, 1 - d_1, 0), \left(\frac{a_4 - a_3}{a_4 + 1}, 0, \frac{a_3 + 1}{a_4 + 1} \right) \text{ and } \left(0, 0, \frac{a_3}{a_4} \right).$$

If we use the conditions for eigenvalues and their associated stability from the previous section then by evaluating the eigenvalues of their associated Jacobian matrices of System (3.4) and (3.5) at these equilibria, we are able to perform local stability analysis and obtain the sufficient conditions of the local stability of these boundary equilibria. The Jacobian matrix for System (3.4) is as follows:

$$\begin{pmatrix} 1 - 2x - y - z & -x & -x \\ \gamma_1 y & \frac{-\gamma_1(-xy^4 - 2xy^2\beta^2 - x\beta^4 + 2a_1yz\beta^2 + d_1y^4 + 2d_1y^2\beta^2 + d_1\beta^4)}{(y^2 + \beta^2)^2} & -\frac{\gamma_1 y^2 a_1}{y^2 + \beta^2} \\ \gamma_2 z & \frac{2\gamma_2 z a_2 \beta^2}{(y^2 + \beta^2)^2} & \frac{\gamma_2(xy^2 + x\beta^2 + a_2y^2 - d_2y^2 - d_2\beta^2)}{y^2 + \beta^2} \end{pmatrix}$$

Then we can substitute our first equilibria, $x = 0$, $y = 0$, and $z = 0$, into our matrix to get:

$$\begin{pmatrix} 1 & 0 & 0 \\ 0 & -\gamma_1 d_1 & 0 \\ 0 & 0 & -\gamma_2 d_2 \end{pmatrix}$$

with corresponding eigenvalues 1, $-\gamma_1 d_1$, and $-\gamma_2 d_2$. We know this boundary equilibria will never be stable because all three eigenvalues can never be negative. Next, we substitute $x = 1, y = 0, z = 0$ into our Jacobian matrix to get:

$$\begin{pmatrix} -1 & -1 & -1 \\ 0 & \gamma_1(1-d_1) & 0 \\ 0 & 0 & \gamma_2(1-d_2) \end{pmatrix}$$

with corresponding eigenvalues $-1, \gamma_1(1-d_1)$, and $\gamma_2(1-d_2)$. In order to be stable, all three must be negative with $d_1 > 1$ and $d_2 > 1$. If one of these conditions does not hold, either $d_1 < 1$ or $d_2 < 1$, then this will be an unstable boundary equilibria. We already noted that in order for all four boundary equilibria to exist for System (3.4), we must have $d_1 < 1$ or $d_2 < 1$, making this one unstable. If we substitute our third boundary equilibria, $x = d_2, y = 0, z = 1 - d_2$, then we have:

$$\begin{pmatrix} -d_2 & -d_2 & -d_2 \\ 0 & \gamma_1(d_2 - d_1) & 0 \\ \gamma_2(1-d_2) & 0 & 0 \end{pmatrix}$$

with corresponding eigenvalues $-\frac{1}{2}d_2 + \frac{1}{2}\sqrt{d_2^2 - 4\gamma_2 d_2 + 4\gamma_2 d_2^2}, -\frac{1}{2}d_2 - \frac{1}{2}\sqrt{d_2^2 - 4\gamma_2 d_2 + 4\gamma_2 d_2^2}$, and $\gamma_1(d_2 - d_1)$. Since the first two eigenvalues are of the form $a \pm \sqrt{b}$ then we can add them and multiply them to check whether they are both positive or negative. When we add the first and second eigenvalues we get $-d_2$ which is enough to ensure us that at least one of them is negative. For both of them to be negative, their product must be positive. We multiply the first and second eigenvalue to get $\gamma_2 d_2(1 - d_2)$. Thus, $d_2 < 1$ would suggest stability. However, we must also consider the third eigenvalue. It is easy to see that $\gamma_1(d_2 - d_1)$ is negative when $d_2 < d_1$. If either $d_2 > 1$ or $d_2 > d_1$ then this boundary equi-

libria does not satisfy the necessary conditions for stability. We can then substitute the values for the fourth boundary equilibria for System (3.4), $x = d_1$, $y = 1 - d_1$, and $z = 0$:

$$\begin{pmatrix} -d_1 & -d_1 & -d_1 \\ \gamma_1(1-d_1) & 0 & -\frac{\gamma_1(1-d_1)^2 a_1}{(1-d_1)^2 + \beta^2} \\ 0 & 0 & \gamma_2 \frac{a_2(1-d_1)^2}{(1-d_1)^2 + \beta^2} - d_2 \end{pmatrix}$$

with corresponding eigenvalues $\frac{(-1+d_1)^2(-d_2+a_4+d_1)+\beta^2(-d_2+d_1)}{(-1+d_1)^2+\beta^2}$, $-\frac{1}{2}d_1 + \frac{1}{2}\sqrt{d_1(d_1-4\gamma_1+4\gamma_1d_1)}$, and $-\frac{1}{2}d_1 - \frac{1}{2}\sqrt{d_1(d_1-4\gamma_1+4\gamma_1d_1)}$. The first eigenvalue can be simplified and set < 0 as a necessary condition for stability or > 0 as a potential condition for an unstable boundary equilibria. For the second and third eigenvalues, we can use the same technique that we used for the previous one. We add them to get $-d_1$ and multiply them to get $\gamma_1 d_1(1-d_1)$. From here, we can see that $d_1 < 1$ is another condition for stability while $d_1 > 1$ would suggest an unstable boundary equilibria.

Next, we use the same process for System (3.5). The Jacobian matrix for System (3.5) is as follows:

$$\begin{pmatrix} 1-2x-y-z & -x & -x \\ \gamma_1 y & -\frac{\gamma_1(-xy^4-2xy^2\beta^2-x\beta^4+2a_1yz\beta^2+d_1y^4+2d_1y^2\beta^2+d_1\beta^4)}{(y^2+\beta^2)^2} & -\frac{\gamma_1 y^2 a_1}{y^2+\beta^2} \\ \gamma_2 z & \frac{2\gamma_2 z a_2 y \beta^2}{(y^2+\beta^2)^2} & \frac{\gamma_2(a_3 y^2+a_3\beta^2-2a_4 z \beta^2+xy^2+x\beta^2+a_2 y^2)}{y^2+\beta^2} \end{pmatrix}$$

Then we can substitute our first equilibria, $x = 0$, $y = 0$, and $z = 0$, into our matrix to get:

$$\begin{pmatrix} 1 & 0 & 0 \\ 0 & -\gamma_1 d_1 & 0 \\ 0 & 0 & -\gamma_2 a_3 \end{pmatrix}$$

with corresponding eigenvalues 1, $-\gamma_1 d_1$, and γ_2 . It is easy to see that all three eigenvalues will never be negative, so this boundary equilibria cannot be stable. Next, we substitute $x = 1$, $y = 0$, and $z = 0$ into our matrix to get:

$$\begin{pmatrix} -1 & -1 & -1 \\ 0 & \gamma_1(1-d_1) & 0 \\ 0 & 0 & \gamma_2(1+a_3) \end{pmatrix}$$

with corresponding eigenvalues -1 , $\gamma_1(1-d_1)$, and $\gamma_2(1+a_3)$. Since the third eigenvalue will always be positive, this boundary equilibria cannot ever be stable. If we substitute the values for our third equilibria, $x = 0$, $y = 0$, $z = \frac{a_3}{a_4}$ we get:

$$\begin{pmatrix} 1 - \frac{a_3}{a_4} & 0 & 0 \\ 0 & -\gamma_1 d_1 & 0 \\ \frac{\gamma_2 a_3}{a_4} & 0 & -\gamma_2(a_3) \end{pmatrix}$$

with corresponding eigenvalues $\frac{a_4 - a_3}{a_4}$, $-\gamma_1 d_1$, and $-\gamma_2 a_3$. Since the second and third eigenvalues will always be negative, stability depends on the sign of the first one. If $\frac{a_3}{a_4} > 1$, it will be negative and this will be a stable boundary equilibria. But if $\frac{a_3}{a_4} < 1$ then it will most likely be unstable. We can then substitute the values for our fourth boundary equilibria, $x = \frac{a_4 - a_3}{a_4 + 1}$, $y = 0$, and $z = \frac{1 + a_3}{a_4 + 1}$:

$$\begin{pmatrix} \frac{a_3 - a_4}{1 + a_4} & \frac{a_3 - a_4}{1 + a_4} & \frac{a_3 - a_4}{1 + a_4} \\ 0 & -\frac{\gamma_1(a_3 - a_4 + d_1 a_4 + d_1)}{1 + a_4} & 0 \\ \frac{\gamma_2(1 + a_3)}{1 + a_4} & 0 & -\frac{\gamma_2(1 + a_3)a_4}{1 + a_4} \end{pmatrix}$$

with one eigenvalue $-\frac{\gamma_1(-a_4 + a_3 + d_1 a_4 + d_1)}{1 + a_4}$. The second and third are of the form $a \pm \sqrt{b}$, so we are primarily concerned with their sum and product. The first eigenvalue will be negative if $0 < \frac{a_4 - a_3}{1 + a_4} < d_1$, making this a necessary condition for stability. From here, we see that this boundary equilibria will be unstable if $\frac{a_4 - a_3}{1 + a_4} > d_1$ or if $a_4 < a_3$, making the same fraction negative. Next, we must also consider the second and third eigenvalues. We add them to get $-\frac{a_4 \gamma_2(a_3 + 1) + a_4 - a_3}{1 + a_4}$ and multiply them to get $-\frac{\gamma(1 + a_3)(a_3 - a_4)}{1 + a_4}$. From this, we can see that $a_4 > a_3$ is a necessary condition for stability while the opposite would cause instability. This is intrinsic to the conditions derived from the first eigenvalues. Note that this boundary equilibria will not exist in our system if $a_3 > a_4$. Finally, we substitute the the last boundary equilibria from System (3.5), $x = d_1$, $y = 1 - d_1$, and $z = 0$:

$$\begin{pmatrix} -d_1 & -d_1 & -d_1 \\ \gamma_1(1 - d_1) & 0 & -\frac{\gamma_1(1 - d_1)^2 a_1}{(1 - d_1)^2 + \beta^2} \\ 0 & 0 & \gamma_2(a_3 + d_1 + \frac{a_2(1 - d_1)^2}{(1 - d_1)^2 + \beta^2}) \end{pmatrix}$$

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with corresponding eigenvalues $\frac{\gamma_2[(d_1-1)^2(d_1+a_2+a_3)+\beta^2(d_1+a_3)]}{(d_1-1)^2+\beta^2}$, $-\frac{1}{2}d_1 + \frac{1}{2}\sqrt{d_1^2 + 4\gamma_1 d_1(d_1-1)}$, and $-\frac{1}{2}d_1 - \frac{1}{2}\sqrt{d_1^2 + 4\gamma_1 d_1(d_1-1)}$. Since the first eigenvalue will never be negative, this boundary equilibria cannot be stable. The conditions for local stability of boundary equilibria for System (3.4) and (3.5) are summarized in Tables 3.2 and 3.3.

BE point	Conditions for stability	Conditions for instability
(0,0,0)	Never	Always
(1,0,0)	$d_1 > 1$ and $d_2 > 1$	$d_1 < 1$; or $d_2 < 1$
$(d_2, 0, 1-d_2)$	$d_2 < d_1$ and $d_2 < 1$	$d_2 > d_1$; or $d_2 > 1$
$(d_1, 1-d_1, 0)$	$d_1 + \frac{a_2(d_1-1)^2}{(-1+d_1)^2+\beta^2} < d_2$ and $d_1 < 1$	$d_1 + \frac{a_2(d_1-1)^2}{(-1+d_1)^2+\beta^2} > d_2$ or $d_1 > 1$

Table 3.2: Specialist Predator (3.4): Local stability conditions for boundary equilibria (BE)

BE point	Conditions for stability	Conditions for instability
(0,0,0)	Never	Always
$(0, 0, \frac{a_3}{a_4})$	$\frac{a_3}{a_4} > 1$	$\frac{a_3}{a_4} < 1$
(1,0,0)	Never	Always
$(\frac{a_4-a_3}{a_4+1}, 0, \frac{1+a_3}{a_4+1})$	$0 < \frac{a_4-a_3}{1+a_4} < d_1$	$\frac{a_4-a_3}{1+a_4} > d_1$; or $a_4 < a_3$
$(d_1, 1-d_1, 0)$	Never	Always

Table 3.3: Generalist Predator (3.5): Local stability conditions for boundary equilibria (BE)

Then the following conditions hold:

1. Both System (3.4) and (3.5) have unstable extinction equilibria (0,0,0).
2. For System (3.4), if (1,0,0) is locally asymptotically stable, then (3.4) has only two equilibrium: (0,0,0) and (1,0,0).
3. For System (3.4), the equilibria $(d_1, 1-d_1, 0)$ and $(d_2, 0, 1-d_2)$ can not be both locally asymptotically stable at the same time.
4. For System (3.5), if $(0, 0, \frac{a_3}{a_4})$ is locally asymptotically stable, then (3.5) does not have the equilibrium $(\frac{a_4-a_3}{a_4+1}, 0, \frac{1+a_3}{a_4+1})$.

5. The big difference between System (3.4) and System (3.5) in the local stability of the boundary equilibria is that both $(1, 0, 0)$ and $(d_1, 1 - d_1, 0)$ are always unstable for (3.5) while they can be locally asymptotically stable for (3.4) under certain conditions. This implies that species z can invade species x and y for (3.5).

Global Dynamics: Extinction and Persistence

Notice that both System (3.4) and (3.5) have the same following subsystem in the case that species z is absent, i.e., $z = 0$

$$\begin{aligned} x' &= x(1 - x - y) \\ y' &= \gamma_1 y(x - d_1) \end{aligned} \tag{3.6}$$

where this subsystem 3.6 is globally stable at $(1, 0)$ if $d_1 > 1$ while it is globally stable at $(d_1, 1 - d_1)$ if $0 < d_1 < 1$.

We can also consider the subsystems of System (3.4) and (3.5) that includes only species x and z as 3.7 and 3.8, respectively

$$\begin{aligned} x' &= x(1 - x - z) \\ z' &= \gamma_2 z(x - d_2). \end{aligned} \tag{3.7}$$

and

$$\begin{aligned} x' &= x(1 - x - z) \\ z' &= \gamma_2 z(a_3 - a_4 z + x). \end{aligned} \tag{3.8}$$

where subsystem 3.7 is globally stable at $(1, 0)$ if $d_2 > 1$ while it is globally stable at $(d_2, 1 - d_2)$ if $0 < d_2 < 1$. The subsystem 3.8 is globally stable at $\left(0, \frac{a_3}{a_4}\right)$ if $a_4 < a_3$ while it is globally stable at $\left(\frac{a_4 - a_3}{1 + a_4}, \frac{a_3 + 1}{1 + a_4}\right)$ if $a_4 > a_3$.

From here, we consider the persistence of a single species in R_+^3 for either System (3.4) or (3.5) if there exists constants $0 < b < B$, such that for any initial condition with $x(0) > 0$ the following inequality holds

$$b \leq \liminf_{\tau \rightarrow \infty} x(\tau) \leq \limsup_{\tau \rightarrow \infty} x(\tau) \leq B.$$

Species x persists in between lower bound b and upper bound B . Similar definitions hold for species y and z .

Then the permanence of a system occurs in R_+^3 if there exists constants $0 < b < B$, such that for any initial condition taken in R_+^3 with $x(0)y(0)z(0) > 0$ the following inequality holds

$$b \leq \liminf_{\tau \rightarrow \infty} \min\{x(\tau), y(\tau), z(\tau)\} \leq \limsup_{\tau \rightarrow \infty} \max\{x(\tau), y(\tau), z(\tau)\} \leq B.$$

All three species persist between lower bound b and upper bound B .

Sufficient conditions for the persistence of a single species, two species, and three species for both System (3.4) and (3.5) are stated in Table 3.4. (Kang and Wedekin 2012)

Persistent Species	Sufficient Conditions for (3.4)	Sufficient Conditions for (3.5)
species x	Always	$\frac{a_3}{a_4} < 1$
species z	$d_1 + \frac{a_2(d_1-1)^2}{(-1+d_1)^2+\beta^2} > d_2$ & $d_1 < 1$ or $d_2 < 1$ & $d_1 > 1$	Always
species x, y	$d_1 < \min\{1, d_2\}$	$\frac{a_3}{a_4} < 1$ & $\frac{a_4-a_3}{1+a_4} > d_1$
species x, z	$d_1 + \frac{a_2(d_1-1)^2}{(-1+d_1)^2+\beta^2} > d_2$ & $d_1 < 1$ or $d_2 < 1 < d_1$	$\frac{a_3}{a_4} < 1$
species x, y, z	$d_1 + \frac{a_2(d_1-1)^2}{(-1+d_1)^2+\beta^2} > d_2$ & $d_1 < 1$ or $d_2 < 1 < d_1$	$\frac{a_3}{a_4} < 1$ & $\frac{a_4-a_3}{1+a_4} > d_1$

Table 3.4: Persistence results of (3.4) and (3.5)

Note that species x , z are always persistent for System (3.4), (3.5) respectively. Since species y feeds on species x for both systems, thus we have the following cases:

1. For System (3.4): The extinction of species y happens when System (3.4) has global stability either at $(d_2, 0, 1 - d_2)$ or at $(1, 0, 0)$, i.e., $d_2 < \min\{1, d_1\}$ or $d_1 > 1$. Since species y feeds on species x , the extinction of species x happens when System (3.4) has global stability at $(1, 0, 0)$, i.e., $d_i > 1, i = 1, 2$.
2. Similarly, for System (3.5), species y goes to extinction if $d_1 > 1$ or $\frac{a_3}{a_4} > 1$ and species x goes to extinction if $a_3 > a_4$.

Sufficient conditions for species extinction for both System (3.4) and (3.5) are summarized in Table 3.5. (Kang and Wedekin 2012)

Extinct Species	Sufficient Conditions for (3.4)	Sufficient Conditions for (3.5)
species x	Never	$\frac{a_3}{a_4} > 1$
species y	$d_2 < \min\{1, d_1\}$ or $d_1 > 1$	$d_1 > 1$ or $\frac{a_3}{a_4} > 1$
species z	$d_2 > 1 + a_2$ or	Never
species x, y	Never	$\frac{a_3}{a_4} > 1$
species y, z	$d_i > 1, i = 1, 2$	Never

Table 3.5: Extinction results of (3.4) and (3.5)

We can see that the conditions for persistence and extinction of (3.4) are highly dependent on parameters d_1 and d_2 . On the other hand, conditions for persistence and extinction of (3.5) are highly dependent on variables a_3 and a_4 , along with d_1 . The results of Table 3.4 and 3.5 are summarized with relative bifurcation diagrams (see Figures 3.4 and 3.5) where G.S. indicates the global stability and L.S. indicates the local stability.

From calculations and Figure 3.4 and 3.5 we can see that the relative growth rates $\gamma_i, i = 1, 2$ do not affect species persistence for both (3.4) and (3.5). The persistence of our IGP model with specialist predator (3.4) is determined by the relative mortality rate of IG prey and predator d_i , while the persistence of our IGP model with generalist predator (3.5) is determined by the availability of outside resource, i.e., a_3 and a_4 . This suggests that System (3.5) has “top down” regulation, and System (3.4) has “bottom up” regulation. Additionally, by comparing Figure 3.4 to Figure 3.5, we can see that (3.5) has much larger region being permanent. This may suggest that IGP model with generalist predator is prone to have coexistence of three species. Analyses also suggest that the persistence of species y requires it being superior competitor to IG predator (Kang and Wedekin 2012).

Multiple Interior Attractors

In this section, we are interested in the potential for multiple attractors for System (3.4) and (3.5). The first situation that we consider is when both systems exhibit permanence, e.g., the values of parameters are in Region **V** for System (3.4) and Region **III** for System

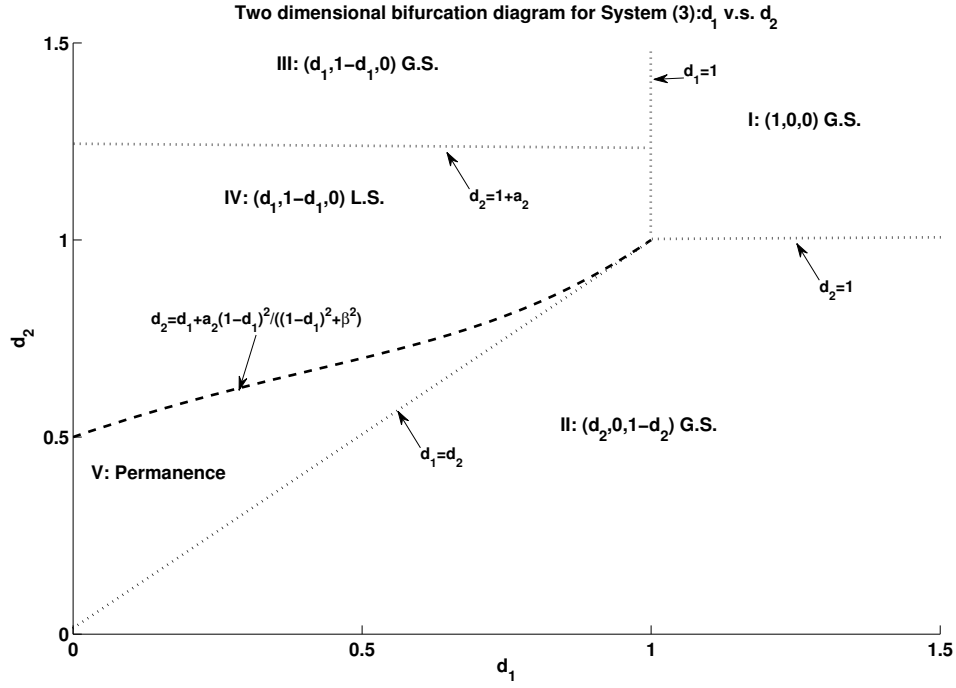


Figure 3.4: Two dimensional bifurcation diagram of d_1 v.s. d_2 for System (3.4).

(3.5). According to the fixed point theorem, the permanence of System (3.4) and (3.5) indicates that they have at least one interior equilibrium. The interesting question is that whether they can have multiple interior equilibria, i.e. multiple interior attractors. The second situation is when System (3.4) and (3.5) exhibit local stability. System (3.4) has local stability at $(d_1, 1 - d_1, 0)$ and System (3.5) has local stability at $(\frac{a_4 - a_3}{1 + a_4}, 0, \frac{1 + a_3}{1 + a_4})$, e.g., the values of parameters are in Region **IV** for System (3.4) and Region **II** for System (3.5). Here, we are interested in whether System (3.4) and (3.5) can have interior equilibria, i.e. an interior attractor. If we consider both the conditions for permanence and local stability then there is the potential for none, one, two, or three multiple interior attractors. Research suggests that System (3.4) may have zero, one or two interior equilibria, and System (3.5) may have zero, one, two or three interior equilibria where one or three occur when System (3.5) is permanent under specific conditions (Kang and Wedekin 2012).

We first consider the potential for multiple attractors of System (3.4). Let $\gamma_1 = 25; \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 = .6; d_1 = .15; d_2 = .54$, then according to the conditions for species persistence and permanence in Table 3.4, we know that System (3.4) is permanent.

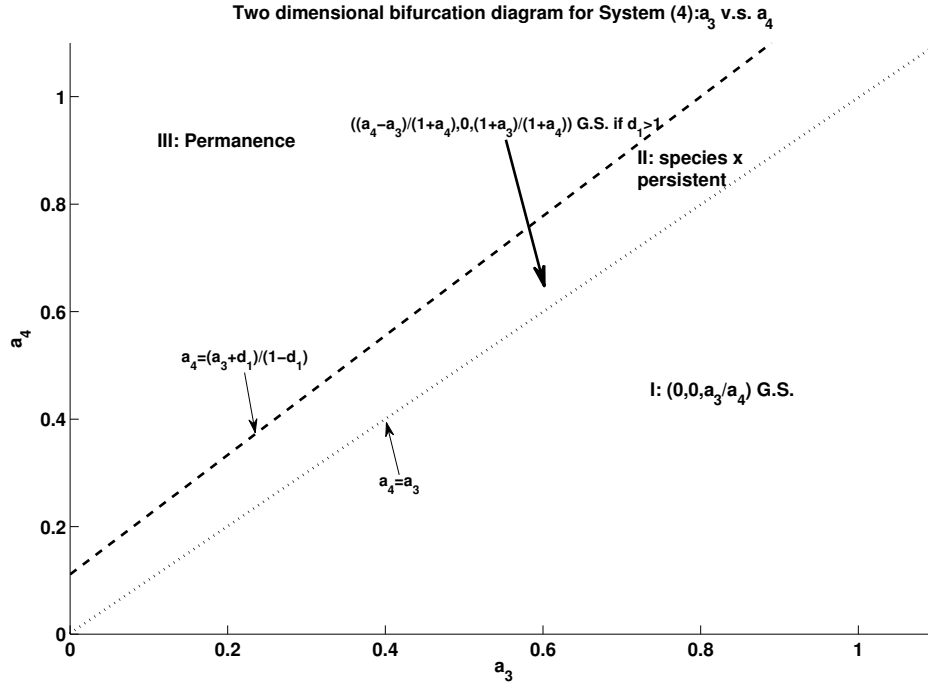
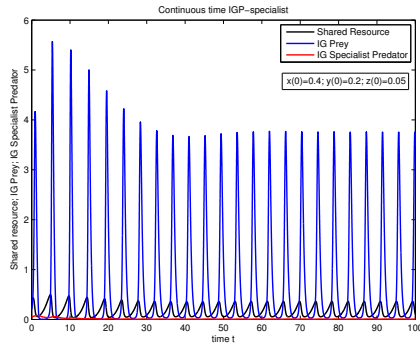


Figure 3.5: Two dimensional bifurcation diagram of a_3 v.s. a_4 for System (3.5).

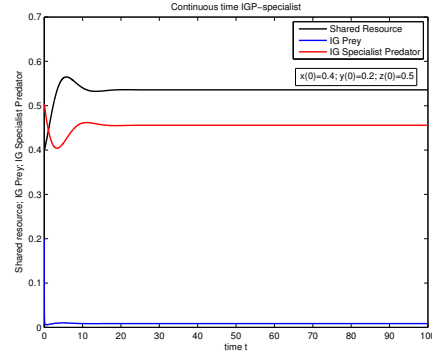
By adjusting initial conditions for z , we can see two interior attractors, one limit cycle (Figure 3.6(a)) and one interior equilibrium (Figure 3.6(b)). Figure 3.6(c) is a 3-dimensional phase plane where the trajectory of System 3.4 enters a limit cycle, and Figure 3.6(d) shows the trajectory of System 3.4 moving toward an interior equilibrium.

Next, let $\gamma_1 = 25; \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 = .01; d_1 = .15; d_2 = .54$. Then according to conditions for local stability of boundary equilibria from Table 3.2, we know that System (3.4) has a locally asymptotically stable boundary equilibrium $(d_1, 1 - d_1, 0) = (0.15, 0.85, 0)$ (Figure 3.7(a)). Additionally, simulations show another attractor dependent on initial conditions which is a locally stable interior equilibrium (Figure 3.7(b))

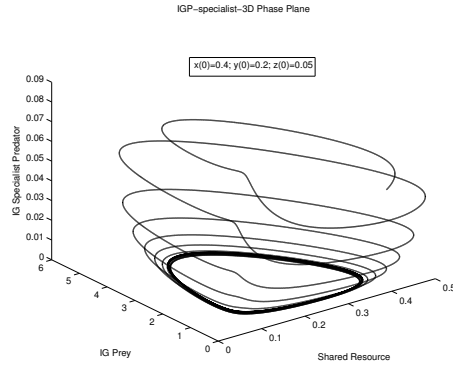
For System (3.5) we are unable to calculate an interior equilibrium when it is locally asymptotically stable at boundary equilibria $\left(\frac{a_4 - a_3}{1 + a_4}, 0, \frac{1 + a_3}{1 + a_4}\right)$. We already noted that System (3.5) may only have up to two interior attractors. Let $\gamma_1 = 25; \gamma_2 = 1; \beta = .15; a_1 = 1; a_2 = .01; a_3 = 0.1; a_4 = 4.5; d_1 = .15$, then according to the conditions for species persistence and permanence in Table 3.4, we know that System (3.5) is permanent. By adjusting initial conditions we can see two interior attractors, one limit cycle (Figure 3.8(a)) and one



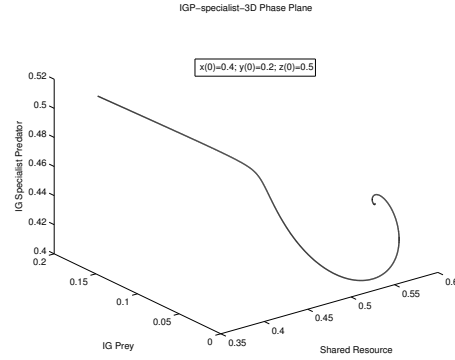
(a) Continuous time series with $x(0) = .4, y(0) = .2, z(0) = .05$.



(b) Continuous time series with $x(0) = .4, y(0) = .2, z(0) = .5$.



(c) 3D Phase Plane with $x(0) = .4, y(0) = .2, z(0) = .05$.



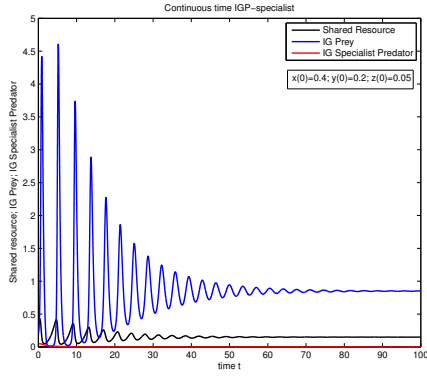
(d) 3D Phase Plane with $x(0) = .4, y(0) = .2, z(0) = .5$.

Figure 3.6: When $\gamma_1 = 25; \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 = .6; d_1 = .15; d_2 = .54$, System (3.4) is permanent with two interior attractors: (a) limit cycle and (b) interior equilibrium

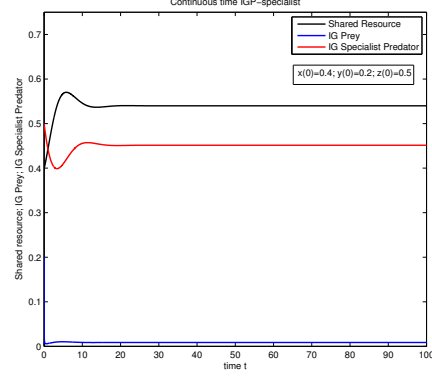
interior equilibrium (Figure 3.8(b)).

Notable Dynamics

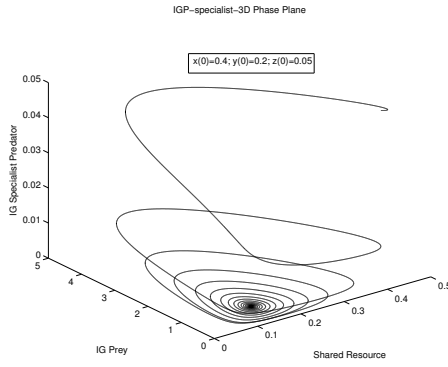
One of the goals of this paper is to analyze the differences in dynamics between specialist and generalist predators in an IGP model. In Chapter 2, we discussed the implications of potential differences in biological control. In this section, we compare System (3.4) and System (3.5) through simulations by simultaneously varying parameter values and initial conditions for both systems. Let $\gamma_1 = 25; \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 = .6; a_3 = 1; a_4 = 20; d_1 = .15; d_2 = .54$, then we know from Figure 3.6(a) that our IGP model with specialist predator will exhibit an interior attractor that is a limit cycle. With initial conditions $x(0) = .4, y(0) = .2, z(0) = .05$, our IGP model with generalist preda-



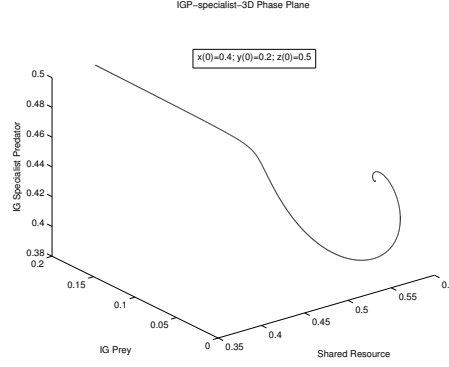
(a) Continuous time series with $x(0) = 0.4, y(0) = 0.2, z(0) = 0.05$.



(b) Continuous time series with $x(0) = 0.4, y(0) = 0.2, z(0) = 0.5$.



(c) 3D Phase Plane with $x(0) = 0.4, y(0) = 0.2, z(0) = 0.05$.

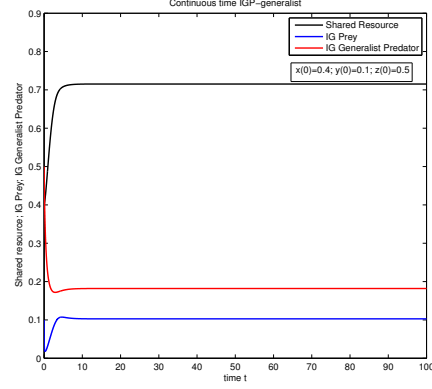
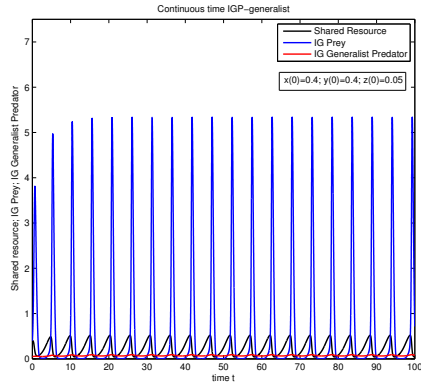


(d) 3D Phase Plane with $x(0) = 0.4, y(0) = 0.2, z(0) = 0.5$.

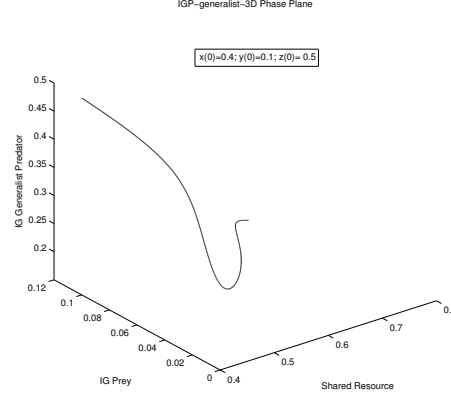
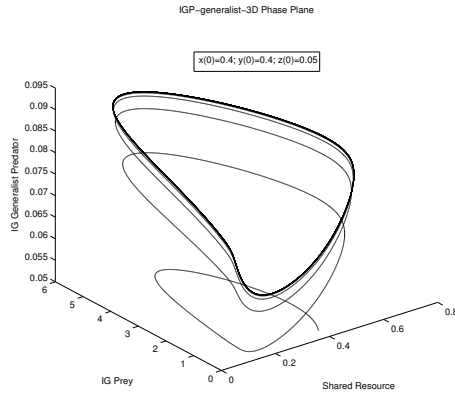
Figure 3.7: When $\gamma_1 = 25; \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 = .01; d_1 = .15; d_2 = .54$, System (3.4) has two attractors: (a) boundary equilibrium $(d_1, 1 - d_1, 0)$ and (b) interior equilibrium.

tor exhibits similar dynamics, an interior attractor that is a limit cycle. However, we are most interested in the change in dynamics when we alter the initial conditions for z , $x(0) = .4, y(0) = .2, z(0) = .5$. System (3.4) now gravitates toward an interior equilibrium (Figure 3.9(c)) while dynamics for System (3.5) remain almost unchanged (Figure 3.9(d)). We can conclude from these simulations that there are drastic differences in the dynamics of an IGP system with specialist predator and generalist predator, notably in their sensitivity to initial conditions.

Next, let $\gamma_1 = 1; \gamma_2 = 5; \beta = .5; a_1 = 1; a_2 = 5; a_3 = 1; a_4 = 2; d_1 = .1; d_2 = 1.2$ with initial conditions $x(0) = .4, y(0) = .2, z(0) = .05$. Notice from 3.10 that System (3.4) exhibits unstable dynamics as all three species oscillate away from an equilibria while



(a) Continuous time series with $x(0) = .4, y(0) = .4, z(0) = .05$. (b) Continuous time series with $x(0) = .4, y(0) = .1, z(0) = .5$.

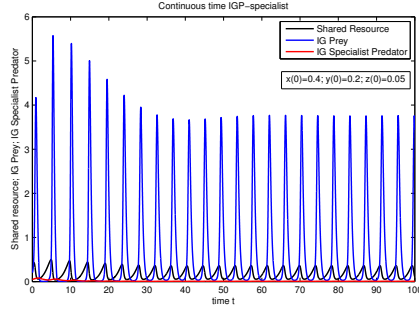


(c) 3D Phase Plane with $x(0) = .4, y(0) = .4, z(0) = .05$. (d) 3D Phase Plane with $x(0) = .4, y(0) = .1, z(0) = .5$.

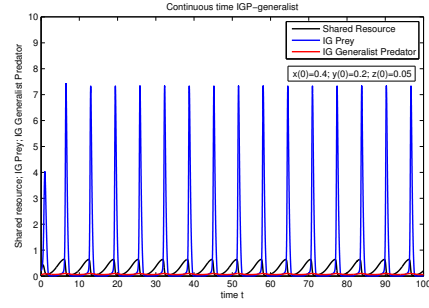
Figure 3.8: When $\gamma_1 = 25; \gamma_2 = 1; \beta = .15; a_1 = 1; a_2 = .01; a_3 = .1; a_4 = 4.5; d_1 = .15$, System (3.5) is permanent with two interior attractors: (a) limit cycle and (b) interior equilibrium.

System (3.5) moves towards an interior attractor. Note that in Figure 3.10(c), the trajectory is oscillating away and not toward from an equilibria at an accelerating rate. In Figure 3.10(d), we see the usual movement approaching an interior equilibrium.

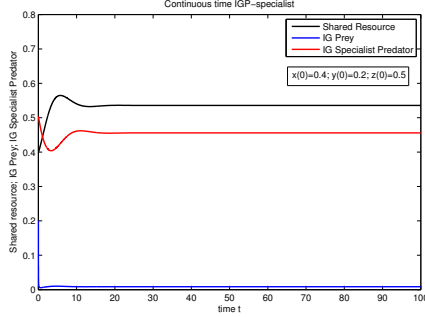
From these simulations, we can predict that System (3.4) will continue to show more complicated dynamics than System (3.5). This can be traced back to the inherent behavior of specialist predators. Thus, biologists must consider the differences between specialists and generalists when attempting to maintain or alter a community. Introducing a specialist predator into an ecosystem for biocontrol purposes where a generalist predator needed may have severely negative effects.



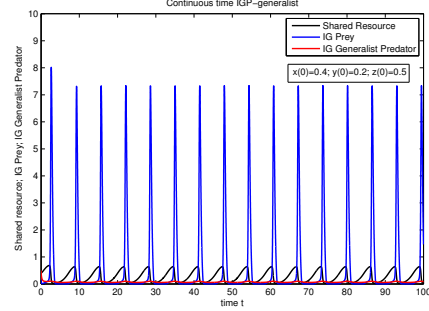
(a) IGP with Specialist Predator $x(0) = .4, y(0) = .2, z(0) = .05$.



(b) IGP with Generalist Predator $x(0) = .4, y(0) = .2, z(0) = .05$.



(c) IGP with Specialist Predator $x(0) = .4, y(0) = .2, z(0) = .5$.



(d) IGP with Generalist Predator $x(0) = .4, y(0) = .2, z(0) = .5$.

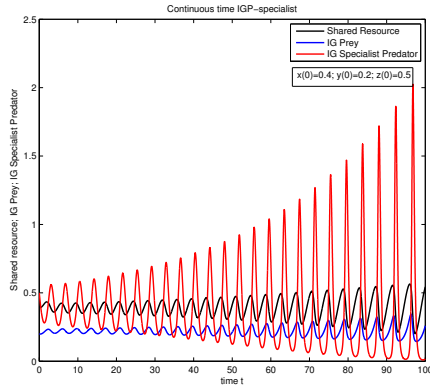
Figure 3.9: When $\gamma_1 = 25; \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 = .6; a_3 = 1; a_4 = 20; d_1 = .15; d_2 = .54$, altering initial conditions exhibits differences in dynamics between IGP models with specialist predator and generalist predator.

3.3 Model Comparison - Continuous and Discrete

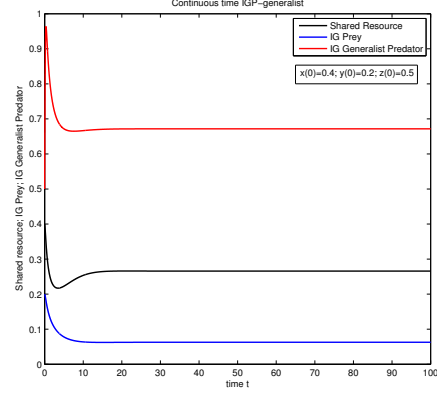
We consider the discrete time-series IGP model for comparison purposes to our analysis of the continuous time-series model. First, consider System (3.4), simplified from System (3.4), by letting $x = \frac{P}{K_p}, y = \frac{a_g G}{r_p}, z = \frac{a_m M}{r_p}, \tau = r_p t, \gamma_1 = \frac{e_g a_g K_p}{r_p}, a_1 = \frac{a_g a_m a}{e_g K_p}, \beta = \frac{r_p}{a_g}, d_1 = \frac{d_g}{e_g a_g K_p}, \gamma_2 = \frac{e_m a_m K_p}{r_p}, a_2 = \frac{a}{a_m K_p}, d_2 = \frac{d_m}{e_m a_m K_p}$. Then the discrete time IGP model with specialist predator is described by:

$$\begin{aligned} x_{t+1} &= x_t e^{(1-x_t-y_t-z_t)} \\ y_{t+1} &= y_t e^{\gamma_1(x_t - \frac{a_1 y_t z_t}{y_t^2 + \beta^2} - d_1)} \\ z_{t+1} &= z_t e^{\gamma_2(x_t + \frac{a_2 y_t^2}{y_t^2 + \beta^2} - d_2)}. \end{aligned} \quad (3.9)$$

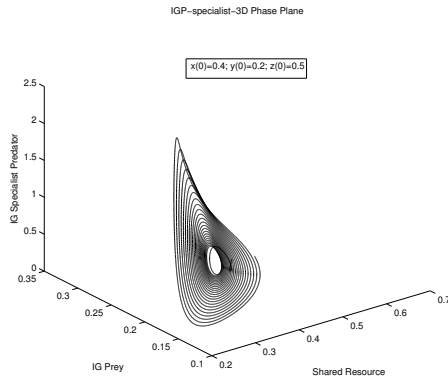
Second, consider System (3.5), simplified from System (3.5), by letting $x = \frac{P}{K_p}, y = \frac{a_g G}{r_p}, z = \frac{a_m M}{r_p}, \tau = r_p t, \gamma_1 = \frac{e_g a_g K_p}{r_p}, a_1 = \frac{a_g a_m a}{e_g K_p}, \beta = \frac{r_p}{a_g}, d_1 = \frac{d_g}{e_g a_g K_p}, \gamma_2 = \frac{e_m a_m K_p}{r_p}, a_2 = \frac{a}{a_m K_p}, a_3 =$



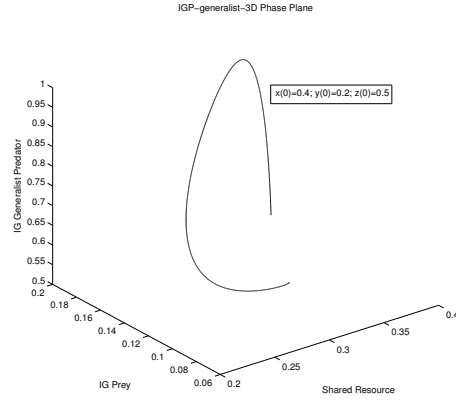
(a) IGP with Specialist Predator $x(0) = .4, y(0) = .2, z(0) = .5$.



(b) IGP with Generalist Predator $x(0) = .4, y(0) = .2, z(0) = .5$.



(c) IGP with Specialist Predator $x(0) = .4, y(0) = .2, z(0) = .5$.



(d) IGP with Generalist Predator $x(0) = .4, y(0) = .2, z(0) = .5$.

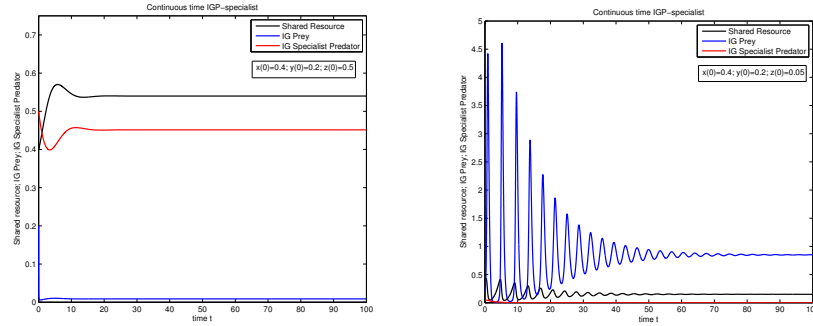
Figure 3.10: When $\gamma_1 = 1; \gamma_2 = 5; \beta = .5; a_1 = 1; a_2 = 5; a_3 = 1; a_4 = 2; d_1 = .1; d_2 = 1.2$: (a) IGP model with specialist predator, unstable dynamics and (b) IGP model with generalist predator, interior equilibrium.

$\frac{r_m}{e_m a_m K_p}, a_4 = \frac{r_p r_m}{K_m a_m^2 e_m K_p}, d_2 = \frac{d_m}{e_m a_m K_p}$. Then the discrete time IGP model with generalist predator is described by:

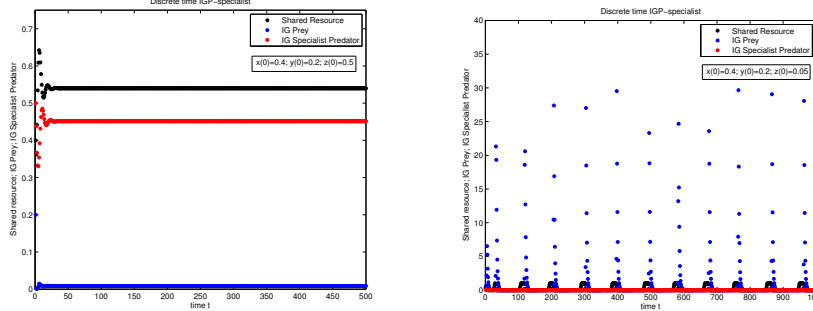
$$\begin{aligned} x_{t+1} &= x_t e^{(1-x_t-y_t-z_t)} \\ y_{t+1} &= y_t e^{\gamma_1(x_t - \frac{a_1 y_t z_t}{y_t^2 + \beta^2} - d_1)} \\ z_{t+1} &= z_t e^{\gamma_2(a_3 - a_4 z_t + x_t + \frac{a_2 y_t^2}{y_t^2 + \beta^2})} \end{aligned} \quad (3.10)$$

In the previous section, we discussed the potential for multiple interior attractors for System (3.4) and (3.5). Here, we will use those results to see if System (3.9) and (3.10) exhibit similar dynamics. Let $\gamma_1 = \ln(25); \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 = .6; d_1 = .15; d_2 = .54$, then we know from Figure 3.7 that initial conditions control the occurrence of a locally

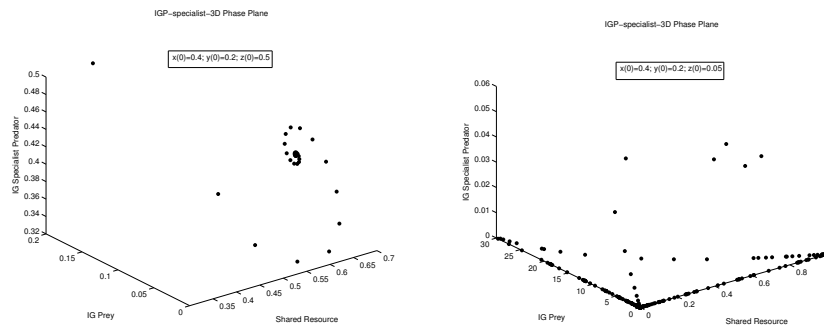
asymptotically stable boundary equilibrium or a locally stable interior equilibrium. For simulation purposes, we let $\gamma_1 = \ln(\gamma_1)$ that we used for continuous time. We can see from Figure 3.11 that the dynamics of our discrete time IGP model with specialist predator are comparable to those of our continuous time model. However, when $z(0) = .05$, System (3.9) does not approach a boundary equilibrium.



(a) Continuous time IGP with Specialist Predator $x(0) = .4, y(0) = .2, z(0) = .5$. (b) Continuous time IGP with Specialist Predator $x(0) = .4, y(0) = .2, z(0) = .05$.



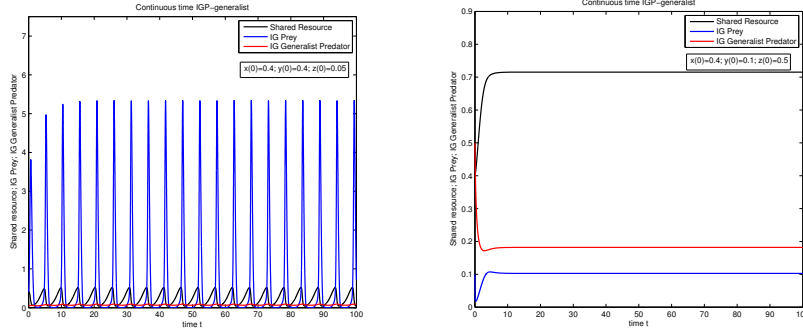
(c) Discrete time IGP with Specialist Predator $x(0) = .4, y(0) = .2, z(0) = .5$. (d) Discrete time IGP with Specialist Predator $x(0) = .4, y(0) = .2, z(0) = .05$.



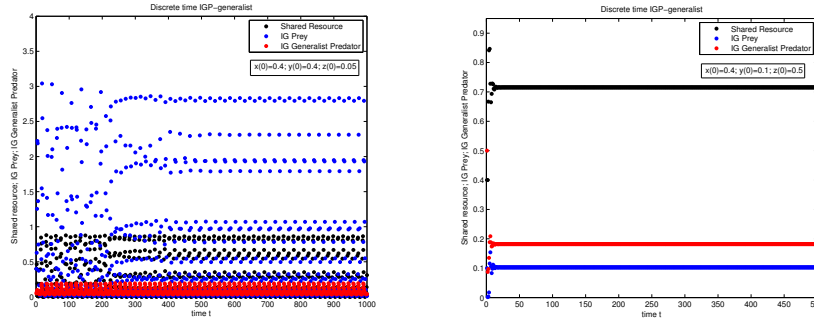
(e) 3D Phase Plane with Specialist Predator $x(0) = .4, y(0) = .2, z(0) = .5$. (f) 3D Phase Plane with Specialist Predator $x(0) = .4, y(0) = .2, z(0) = .05$.

Figure 3.11: When $\gamma_1 = \ln(25); \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 = .6; d_1 = .15; d_2 = .54$, we see comparable dynamics between continuous time-series and discrete time-series for IGP with specialist predator.

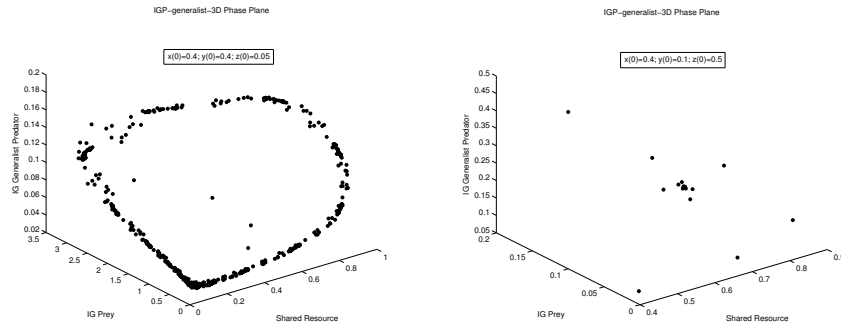
Now let $\gamma_1 = \ln(25); \gamma_2 = 1; \beta = .15; a_1 = 1; a_2 = .01; a_3 = .1; a_4 = 4.5; d_1 = .15; d_2 = .54$, then we already know that System (3.5) is permanent. Additionally, from Figure 3.8 we know that we have two interior attractors, one limit cycle and one interior equilibrium. We notice the same dynamics for discrete time IGP with generalist predator (see Figure 3.12).



(a) Continuous time IGP with Generalist Predator $x(0) = .4, y(0) = .4, z(0) = .05$. (b) Continuous time IGP with Generalist Predator $x(0) = .4, y(0) = .1, z(0) = .5$.



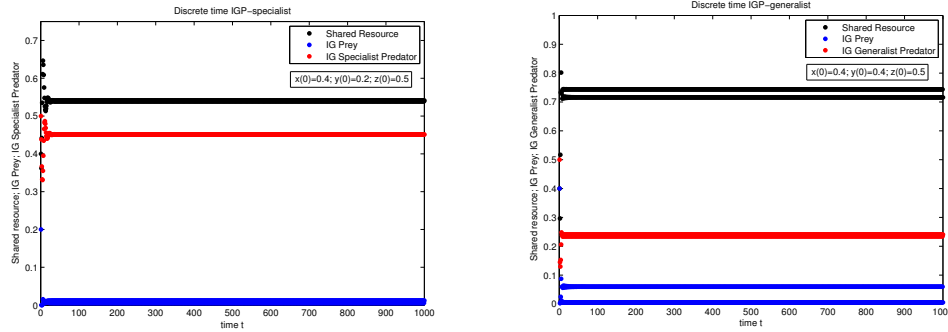
(c) Discrete time IGP with Generalist Predator $x(0) = .4, y(0) = .4, z(0) = .05$. (d) Discrete time IGP with Generalist Predator $x(0) = .4, y(0) = .1, z(0) = .5$.



(e) 3D Phase Plane with Generalist Predator $x(0) = .4, y(0) = .4, z(0) = .05$. (f) 3D Phase Plane with Generalist Predator $x(0) = .4, y(0) = .1, z(0) = .5$.

Figure 3.12: When $\gamma_1 = \ln(25); \gamma_2 = 1; \beta = .15; a_1 = 1; a_2 = .01; a_3 = .1; a_4 = 4.5; d_1 = .15$, we see comparable dynamics between continuous time-series and discrete time-series for IGP with generalist predator.

The famous model for discrete time growth, Ricker's model, suggests that a system will crash when the growth rate increases beyond a certain threshold. We can check to see if this theory holds for System (3.9) and (3.10) by altering γ_1 and γ_2 . Let $\gamma_1 = \ln(250)$ for System (3.4) and (3.5). We see from Figure 3.13 that both systems maintain three species coexistence.



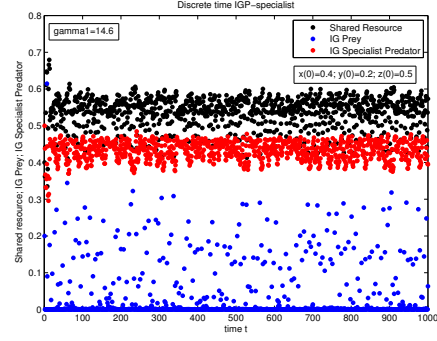
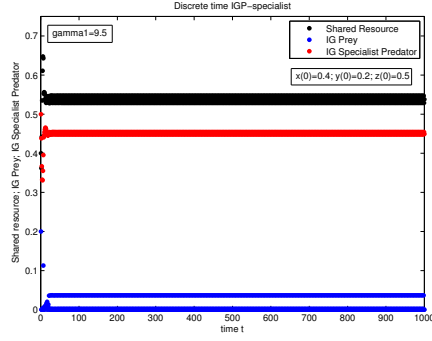
(a) Discrete time IGP with Specialist Predator with $\gamma_1 = \ln(250); \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 = .01; d_1 = .15; d_2 = .54$ and $x(0) = .4, y(0) = .01; a_3 = .1; a_4 = 3.5; d_1 = .15$ and $x(0) = .2, z(0) = .5$.
(b) Discrete time IGP with Generalist Predator with $\gamma_1 = \ln(250); \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 = .01; d_1 = .15; d_2 = .54$ and $x(0) = .4, y(0) = .01; a_3 = .1; a_4 = 3.5; d_1 = .15$ and $x(0) = .2, z(0) = .5$.

Figure 3.13: When $\gamma_1 = \ln(250)$ we have three-species persistence. This contradicts Ricker's model that suggests inevitable species extinction of either one (specialist predator) or two (generalist predator) species.

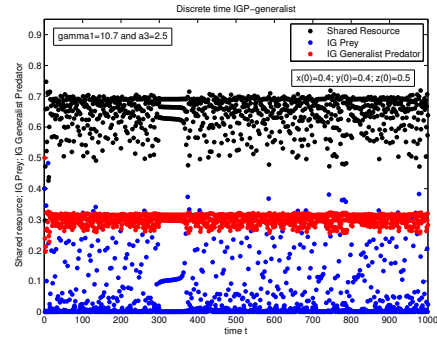
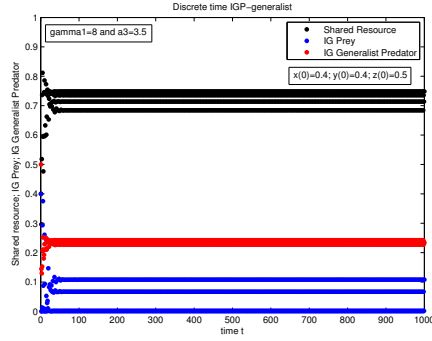
Next, let $\gamma_1 = 8.5$ and then $\gamma_1 = 14.6$ for System (3.9), and let $\gamma_1 = 8$ and then $\gamma_1 = 10.7$ for System (3.10). Dynamics resemble those of Ricker's model as growth rate increases (see Figure 3.14), and the systems do not crash when γ_1 is increased significantly without the natural log. In fact, we see dynamics that resemble those of Ricker's model. As γ_1 increases, species begin to approach limit cycles and eventually resemble chaotic behavior.

3.4 Semi-Discrete

We know the most realistic time series model for the system that we are interested in is the semi-discrete time series. Unfortunately, model complexity prohibits a simplified analysis, and we must use our original model. Recall the semi-discrete time series model that we derived in Chapter 2, System (3.11)-(3.14), with additional parameter values from Table 3.6 to indicate differences in dynamics between seasons.



(a) Discrete time IGP with Specialist Preda- (b) Discrete time IGP with Specialist Preda-
tor with $\gamma_1 = 8.5; \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 =$ tor with $\gamma_1 = 14.6; \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 =$
 $.01; d_1 = .15; d_2 = .54$ and $x(0) = .4, y(0) = .01; a_3 = .1; a_4 = 2.5; d_1 = .15$ and $x(0) =$
 $.4, z(0) = .5.$ $.4, y(0) = .4, z(0) = .5..$



(c) Discrete time IGP with Generalist Preda- (d) Discrete time IGP with Generalist Preda-
tor with $\gamma_1 = 8; \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 = .01; a_3 =$ tor with $\gamma_1 = 10.7; \gamma_2 = 1; \beta = .1; a_1 = 1; a_2 =$
 $.1; a_4 = 3.5; d_1 = .15$ and $x(0) = .4, y(0) = .01; a_3 = .1; a_4 = 2.5; d_1 = .15$ and $x(0) =$
 $.4, z(0) = .5..$ $.4, y(0) = .4, z(0) = .5.$

Figure 3.14: Interesting dynamics when we alter γ_1 .

Parameters	Biological Meanings
d_{g2}	external mortality rate of IG prey in the summer
d_{g3}	external mortality rate of IG prey in the fall
s_g	survival rate of IG prey in egg form
s_p	survival ratio of resource over the winter
q	storage ratio of resource biomass

Table 3.6: Additional Parameters

Consider $P(\tau), G(\tau), M(\tau)$ to be the biomass of plant, herbivore and predator at time τ , then our semi-discrete model is as follows:

• **Spring:**

$$\begin{aligned}
\frac{dP(\tau)}{d\tau} &= r_p P \left[1 - \frac{P}{K_p} \right] \\
\frac{dM(\tau)}{d\tau} &= r_m M \left[1 - \frac{M}{K_m} \right] \\
\tau &\in [0, t_{sp}], P(0) = (1 - q)P_t + s_p q P_t e^{-a_m M_t(t_{sp} + t_{su} + t_f)}, M(0) = M_t
\end{aligned} \tag{3.11}$$

The output of (3.11) is

$$P_t(t_{sp}) = P(t_{sp}), M_t(t_{sp}) = M(t_{sp}).$$

• **Summer:**

$$\begin{aligned}
\frac{dP(\tau)}{d\tau} &= r_p P \left[1 - \frac{P}{K_p} \right] - a_g P G \\
\frac{dG(\tau)}{d\tau} &= G [e_g a_g P - d_g] \\
\frac{dM(\tau)}{d\tau} &= r_m M \left[1 - \frac{M}{K_m} \right] \\
\tau &\in [0, t_{su}], P(0) = P_t(t_{sp}), G(0) = s_g G_{t-1}(1), M(0) = M_t(t_{sp})
\end{aligned} \tag{3.12}$$

The output of (3.12) is

$$P_t(t_{sp} + t_{su}) = P(t_{su}), G_t(t_{sp} + t_{su}) = G(t_{su}), M_t(t_{sp} + t_{su}) = M(t_{su}).$$

• **Fall:**

$$\begin{aligned}
\frac{dP(\tau)}{d\tau} &= r_p P \left[1 - \frac{P}{K_p} \right] \\
\frac{dG(\tau)}{d\tau} &= -d_g G - \frac{a G^2 M}{G^2 + b^2} \\
\frac{dM(\tau)}{d\tau} &= r_m M \left[1 - \frac{M}{K_m} \right] + \frac{a e_m G^2 M}{G^2 + b^2} \\
\tau &\in [0, t_f], P(0) = P_t(t_{sp} + t_{su}), G(0) = G_t(t_{sp} + t_{su}), M(0) = M_t(t_{sp} + t_{su})
\end{aligned} \tag{3.13}$$

The output of (3.13) is

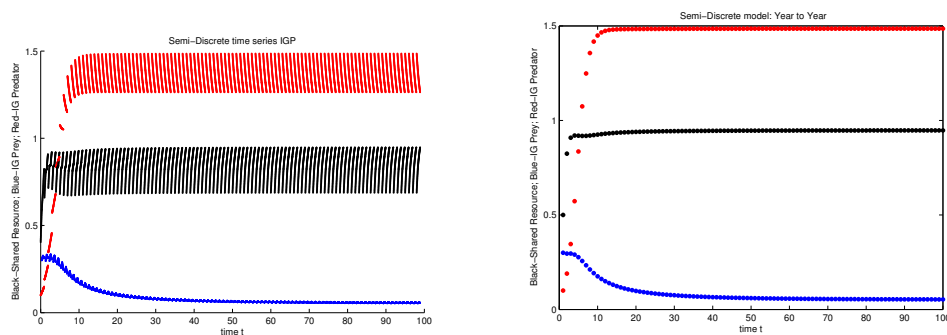
$$P_t(1) = P(t_f), G_t(t_{sp} + t_{su} + t_f) = G(t_f), M_t(t_{sp} + t_{su} + t_f) = M(t_f).$$

• **Winter:**

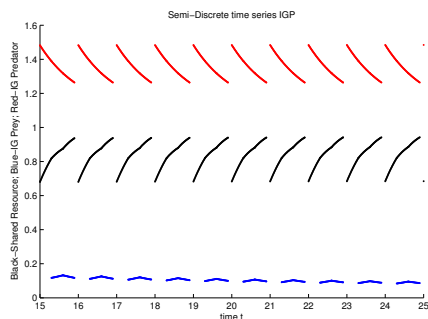
$$\begin{aligned}
P_{t+1} &= P_t(1) \\
G_{t+1} &= G_t(1) = s_g G_t(t_{sp} + t_{su} + t_f) \\
M_{t+1} &= M_t(1) = M_t(t_{sp} + t_{su} + t_f) + q P_{t+1} [1 - e^{-a_m M_t(t_{sp} + t_{su} + t_f)}]
\end{aligned} \tag{3.14}$$

where spring follows from the outputs of winter.

We have focused on the ideas of permanence and persistence so far. Since we are not dealing with a rescaled model, it is more difficult to identify sufficient conditions for either. Thus, we can begin with parameter values from simulations that suggest permanence for our three-species system. Let $r_p = 2.5; K_p = 1; r_m = .5; K_m = 1; a_g = 1.2; a_m = 1.2; a = 0.5; b = 0.5; e_g = 0.5; e_m = 0.1; d_{g2} = 0.1; d_{g3} = 0.1; s_g = 0.95; s_p = 0.4; q = 0.3$ with initial conditions $P(0) = 0.5; G(0) = .3$; and $M(0) = 0.1$. We can see clearly from Figure 3.15 that we should expect three-species permanence under the given conditions.



(a) Semi-discrete time series with $a = 0.5, b = 0.5$. (b) Semi-discrete time series, end of year population density.

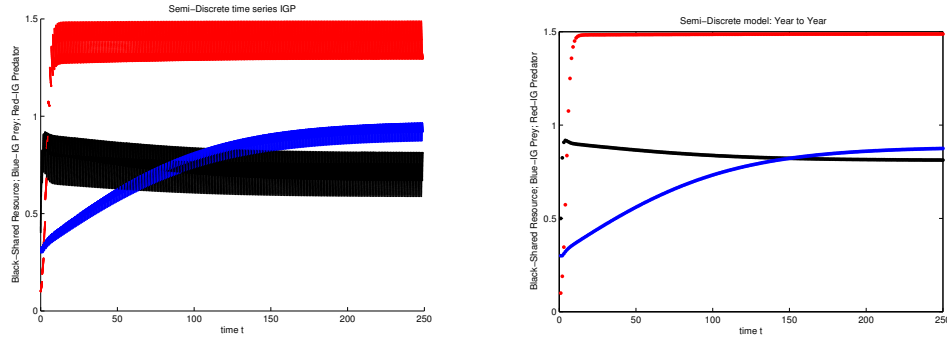


(c) Semi-discrete time series zoomed in to see within year dynamics.

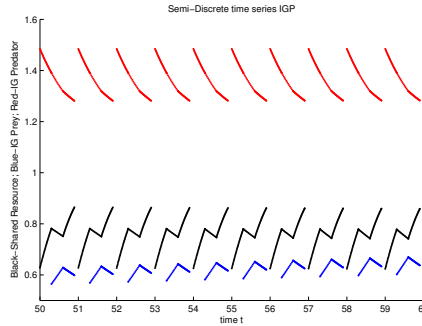
Figure 3.15: Semi-discrete time series with $r_p = 2.5; K_p = 1; r_m = .5; K_m = 1; a_g = 1.2; a_m = 1.2; a = 0.5; b = 0.5; e_g = 0.5; e_m = 0.1; d_{g2} = 0.1; d_{g3} = 0.1; s_g = 0.95; s_p = 0.4; q = 0.3$ and initial conditions $P(0) = 0.5; G(0) = .3$; and $M(0) = 0.1$.

From here we look for the parameters that have the largest effect on the dynamics of System (3.11)-(3.14). Recall the concept of functional response from Chapter 2. We know that a type III functional response will have the most complicated dynamics. From System (3.11)-(3.14), we can alter a and b , both part of the type III functional response of IG

predator to herbivore. We know from Table 3.1 that a is the maximum herbivore population killed by the IG predator. Consider the same conditions from Figure 3.15, but let $a = 0.05$. We see from simulations that this will prevent the overkilling of herbivore by IG predator (see Figure 3.16). We also see more interesting fluctuations in dynamics throughout the year, the continuous part of the semi-discrete time series (see Figure 3.16(c)) During a single year, spring-winter, the biomass of the shared resource decreases when the IG prey becomes active in the summer then increases when IG prey biomass decreases in the fall.



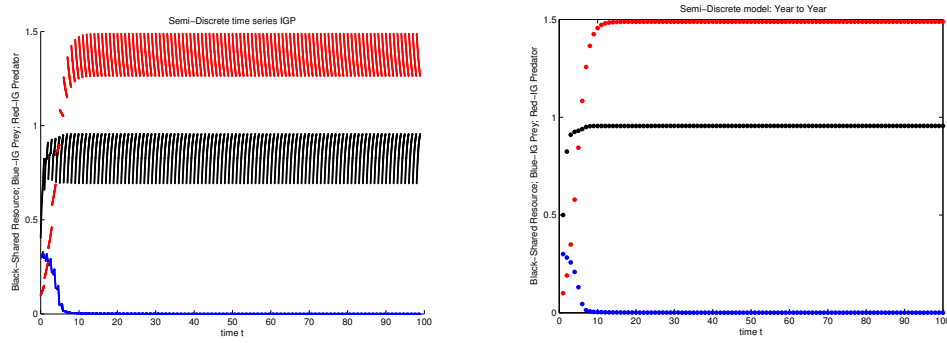
(a) Semi-discrete time series with $a = 0.05, b = 0.5$. (b) Semi-discrete time series, end of year population density.



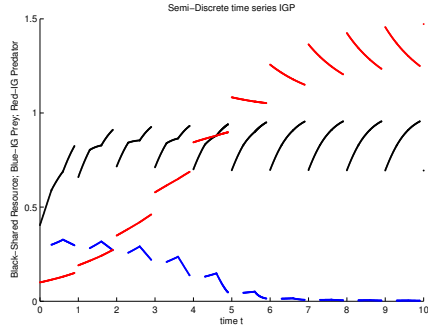
(c) Semi-discrete time series zoomed in to see within year dynamics.

Figure 3.16: Semi-discrete time series with $r_p = 2.5; K_p = 1; r_m = .5; K_m = 1; a_g = 1.2; a_m = 1.2; a = 0.05; b = 0.5; e_g = 0.5; e_m = 0.1; d_{g2} = 0.1; d_{g3} = 0.1; s_g = 0.95; s_p = 0.4; q = 0.3$ and initial conditions $P(0) = 0.5; G(0) = .3$; and $M(0) = 0.1$.

Next let $b = 0.05$. We know from Table 3.1 that b is the herbivore density at which the population killed by the IG predator reaches half of its maximum. Thus, when b decreases significantly the herbivore population should eventually die out (see Figure 3.17). Note that parameter values for a and b play a significant role in the behavior of System (3.11)-(3.14). This tells us that the addition of a type III functional response between IG



(a) Semi-discrete time series with $a = 0.5, b = 0.05$. (b) Semi-discrete time series, end of year population density.



(c) Semi-discrete time series zoomed in to see within year dynamics.

Figure 3.17: Semi-discrete time series with $r_p = 2.5; K_p = 1; r_m = .5; K_m = 1; a_g = 1.2; a_m = 1.2; a = 0.5; b = 0.05; e_g = 0.5; e_m = 0.1; d_{g2} = 0.1; d_{g3} = 0.1; s_g = 0.95; s_p = 0.4; q = 0.3$ and initial conditions $P(0) = 0.5; G(0) = .3$; and $M(0) = 0.1$.

prey and IG predator may determine the potential for none, one, two, or three species persistence, and it most likely alters dynamics significantly from a system that only includes type I.

3.5 Discussion

An analysis of simple community modules such as three-species IGP will help to provide a useful bridge between the thoroughly analyzed two-species dynamics and the excessively complex multi-species world that ecologists hope to understand (Holt and Polis 1997). Mathematical models have been useful in identifying sufficient conditions for coexistence and persistence which may provide some insights and help conservation biologists to identify the leading causes for species extinction. The mathematical analysis of our three-species IGP system is performed similarly to that of a two-species predator-prey

system, but dynamics are significantly more complicated. The addition of a type III functional response makes our model more realistic than that of Holt and Polis (1997), but we also create the potential for additional equilibria and attractors. From current research, we can conclude that our continuous IGP model with either specialist or generalist predator best describes the IGP subsystem of IG predator, IG prey, and shared prey. Ideally, we are able to compare results to those of Holt and Polis (1997) who were limited to Holling type I functional response and a specialist IG predator.

From Table 3.4 we are able to determine sufficient conditions for three species coexistence, and Figure 3.4 and 3.5 suggest the driving parameters of dynamics. While it is difficult to rescale our conditions back to the original parameters, we can see that slight changes to specific variables(d_1 and d_2 for System 3.4; a_3 and a_4 for System 3.5) will likely lead to species extinction. Results indicate that the persistence of IGP with specialist predator is more likely controlled by the relative mortality rates of IG prey and predator d_i , while IGP model with generalist predator is more likely determined by the availability of outside resource, i.e., a_3 and a_4 . Generalist predators thrive on a variety of food sources. Thus, they are more likely to be affected by changes in the amount of outside resources. We can see from (3.5) that a_3 and a_4 are not affected by changes in x and y . Since specialist predators have narrower diets, they are more affected by changes in their own population and IG prey populations. Systems with specialist predator typically display more complicated dynamics while those with generalist predator are prone to have more stable dynamics. Additionally, and IGP system with generalist predator is prone to permanence. This has important implications in conservation biology and management efforts. If biologists can predict persistence, coexistence, or extinction from the addition of a specialist vs. generalist predator, simulations will aid in the decision making process.

Holt and Polis (1997) showed the potential for alternative stable states, general criteria for the coexistence and the increased likelihood of unstable population dynamics with systems involving IGP. We already saw that and IGP system with specialist predator is prone to unstable dynamics while an IGP system with generalist predator is prone to

coexistence. Holt and Polis (1997) showed the only alternative stable states (i.e., multiple attractors) are the locally stable equilibria $(x, y, 0)$ and $(x, 0, z)$ while the alternative stable states for System (3.4) can be either two interior attractors or two attractors where one is a boundary attractor $(d_1, 1 - d_1, 0)$ and the other is an interior attractor. This big difference is due to the fact that (3.4) has a type III function responses between IG prey and specialist IG predator which can also lead to multiple interior attractors with more complicated dynamical patterns including multiple stable limit cycles. One major difference between our models and the Holt-Polis model is that our models can have both boundary and interior attractors under certain conditions while the existence of an interior attractor indicates the permanence in the Holt-Polis model. Holt and Polis (1997) conclude that for coexistence, the IG prey has to be superior to the IG predator at competing for the shared resource. This remains true for System 3.4 and 3.5 where species y will persist only if it is superior to competitor IG predator (Kang and Wedekin 2012). Analyses confirm that these dynamics are due to the inclusion of a type III functional response (Kang and Wedekin 2012).

The continuous time series model is limited to populations with overlapping generations. For a system containing an insect with distinct age-structures, this is not necessarily accurate. Results do not show changes in dynamics between seasons. Nor do they suggest potentially large fluctuations from year to year. Simulations show similar dynamics for our discrete model which suggests model accuracy for both time-series models. However, a discrete time model is limited to a single output per year, and we are more likely to notice chaotic behavior. In a discrete model, whether we consider $t + 1$ to be a year or a single season, we are unable to include seasonal shifts in dynamics. Certain species are only active during specific times of the year, and it is impossible to include interaction changes in a discrete model. Model simulations for our semi-discrete model suggest promising results for future analyses. It is common that system dynamics vary seasonally. In a semi-discrete model, we can include differences in continuous seasonal dynamics due to species interactions occurring at certain times of the year. Additionally, we can consider discrete changes that often accompany changes in season. Thus, it is safe to say that future IGP modeling will begin to resemble this approach, and analyses will

most likely prove that a semi-discrete model will be most suited for modeling an IGP subsystem with stage-structures. While dynamics between continuous and discrete models are comparable, semi-discrete dynamics are more likely to resemble nature and accurately predict species behavior in the future.

SPATIAL SYNCHRONY

Patrick Moran first proposed the idea that outside factors can synchronize fluctuations among spatially separated populations (Moran 1953). Moran studied the oscillatory pattern of the lynx across all of Canada. The lynx is known to feed almost exclusively on the hare, or snowshoe rabbit. Previous studies by Lotka and Volterra suggest that oscillations in population density would be expected under such circumstances. We saw this oscillatory pattern caused by a predator-prey relationship in Chapter 3. Predator populations react to changes in prey populations, and prey populations similarly react to changes in predator populations. Moran (1953) realized that peaks occurred simultaneously in different geographic areas. Synchronizations were not due to a lag effect where peaks in population densities in one area would spark a peak in an adjacent, but disjunct, space. Moran concluded that the findings of his studies were consistent with the idea that weather is the main synchronizing agent for lynx populations. However, it is difficult to tell if there is some other natural phenomenon causing it. Synchronization occurs at all different trophic levels, and it is often difficult to isolate the cause.

Masting is defined as the intermittent production of a large crop. Mast seasons typically occur every four or five years, and masts frequently occur simultaneously across vast geographic terrains. A study by Haynes et al. (2009) suggests that the effects of a synchronized mast may transfer through trophic levels by means of consumer-resource interactions. In fact, they traced oscillations in gypsy moth (*Lymantria dispar*) populations back to masting. We know from Chapter 2 that the gypsy moth is part of an intraguild predation subsystem comprised of the oak (*Quercus* spp.), white-footed mouse (*Peromyscus leucopus*), and gypsy moth. Haynes et al. (2009) identified this as an ideal system to study the interactions between Moran effects and synchronization via consumer-resource interactions.

The gypsy moth has become a major pest in North America. Outbreaks are known

to occur simultaneously over a vast landscape. These outbreaks have caused excessive forest defoliation in the northeast, and populations continue to spread. This has ignited a wide-scale interest in stopping or slowing the spread of the spatial extent of gypsy moths. Since synchronizations can be traced back to mast seasons, ecologists have thoroughly studied the susceptibility of forests to gypsy moth expanse. The Slow the Spread Foundation uses extensive analyses and monitoring to determine appropriate management methods.

Synchronized Masting

We know that masting occurs intermittently and synchronously, but we have not thoroughly addressed why this happens. Questions arise over why reproductive efforts by masting plant species occur sporadically and why these variations are synchronized (Schauber 2000). We also mentioned that synchronizations transcend beyond the population level. Haynes et al. (2009) suggest that this is the result of consumer-resource interactions.

Schauber (2000) adheres to the hypothesis that masting occurs because of a shift in resource allocation from growth/storage to reproduction (Koenig and Knops 2000), making it an evolved reproductive strategy for certain plants. Masting may also affect the response behaviors of seed-consumers. Seed-consumers may benefit greatly during masting seasons, and this effect can indirectly affect other ecosystem components (Schauber 2000, Haynes et al. 2009). For purposes of our study, we acknowledge that these indirect effects ultimately spark damaging insect outbreaks.

In the absence of direct communication among plants, Schauber (2000) suggests that there must be some outside factor that causes widespread synchronized seed production. Otherwise, masting seasons would not occur simultaneously across large regions. Synchronizing cues must be spatially consistent and easily detected by plants. Similar to Moran (1953), Schauber attributes this, at least partially, to weather conditions.

Now that we are familiar with the causes and abundant effects of synchronized masting, we can address the damage done by synchronized insect outbreaks. This is possi-

ble because of the indirect effects of masting. Synchronization is not limited to producers and seed-consumers.

4.1 Invasive Pests

Forests in the Eastern United States have proved to be extremely vulnerable to invasions by exotic insects (Morin et al. 2005). Even as ecologists work adamantly to slow and prevent them, these invasions continue to threaten the productivity and stability of forest ecosystems (Liebhold et al. 1995). An exotic species typically follows the same basic process: 1) arrival, 2) becoming established, and 3) spreading (Dobson and May 1986). Unfortunately, accidental introduction of invasive pests has become increasingly prevalent over the last two centuries (Liebhold et al. 1992). This is highly attributed to exponential rate of increased human mobility. Once a species becomes established, it is important to identify the causes of spread.

Gypsy Moth

The gypsy moth is one of the most destructive invasive insects, responsible for widespread forest defoliation and eventually tree mortality. In its caterpillar stage, the pest is capable of destroying millions of acres of trees in a single season. The gypsy moth was introduced to United States near Boston, Massachusetts in the late 1860s. Since then, they have spread across much of the northeastern United States and parts of Canada. Their presence currently extends as far south as Virginia and North Carolina and as far west as Ohio. They are also found in Michigan due to a second accidental introduction. Since gypsy moths are extremely damaging pests, it is important to understand the underlying mechanisms of their outbreaks and continuous spread (Liebhold et al. 1992).

Gypsy moth outbreaks are known to occur at almost the same time at different locations across the northeastern US (Hanski and Woiwood 1993). The white-footed mouse, a prime predator of the gypsy moth pupae, rely on acorns as a major winter food source. Thus, indirect effects of acorn masting seasons are hypothesized to control the start of gypsy moth outbreaks (Schauber 2000). Recall the dynamics of the three-species IGP

subsystem from Chapter 3. Acorn production in the fall is known to be a reliable predictor of the abundance of the white-footed mouse in oak forests for the following summer (Elkinton et al. 1996). Predation by the white-footed mouse is believed to regulate gypsy moth outbreaks by maintaining gypsy moth populations at low-density and prolonging time between outbreaks (Elkinton et al. 1996). We see from Figure 4.1 that masting seasons are coupled with high white-footed mouse population densities. Increased predation on gypsy moth pupae following mast seasons prolongs time before the next outbreak. Regional synchrony in masting seasons has thus been targeted to explain the synchrony of gypsy moth outbreaks. Therefore, synchronized mast seasons across the northeastern United States will contribute to extremely damaging outbreaks.

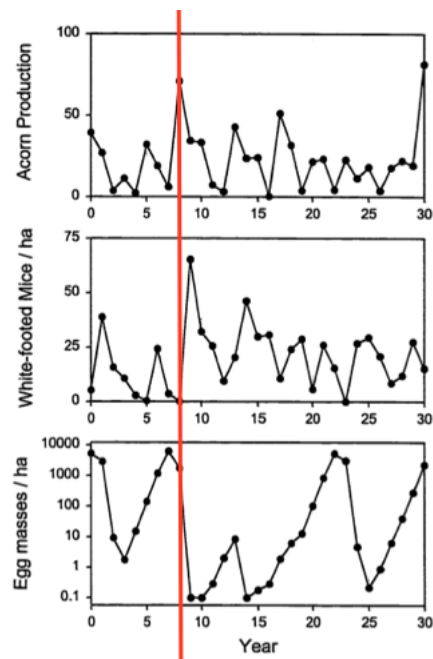


Figure 4.1: Population fluctuations of oak, white-footed mouse, and gypsy moth. (Schauber 2000)

Now that masting is a known cause for continued forest defoliation, efforts can be directed toward prevention and management. The oak is identified as a primary host species for gypsy moths. Thus, forests dominated by oaks or other preferred species are more susceptible to invasions. Since the spread of gypsy moths is relatively slow, it is possible to manage with the correct knowledge. However, gypsy moths also feed on a wide

variety of tree species (not only oak). Thus, it is possible that populations will eventually invade most of the United States and Canada (Liebhold et al. 1992).

4.2 Prevention Efforts

Scientists have recognized that complete eradication of gypsy moths is more or less impossible at this point, but knowledge of when various areas will become infected would be useful when planning for forest management (Liebhold et al. 1992).

Geographic Information System

Geographic Information Systems (GIS) have been thoroughly utilized in the fight against gypsy moths. Data is collected both on land and using aerial imaging techniques. It is then compiled to provide geographically located data that aids in the decision making process for gypsy moth management. A GIS provides scientists with the abilities to store, retrieve, process, and display spatially referenced data. Often, the final product is the most easily accessible and readily useable.

Significant effort has been spent documenting the current spatial extents of gypsy moth defoliation. First, GIS can be used for a visual representation of gypsy moth spread. The most basic map shows the expansion of gypsy moths out of the northeast over the past century (Figure 4.2). Maps were compiled using basic lists of infested counties, and modifications can be used to calculate the rate of spread.

We see from Figure 4.2 that the spread of gypsy moth infestation does not seem to be slowing down by itself. Maps like these are used as "quarantine maps" to identify the annual distribution of a general infected area. Data used to create these maps are used to calculate the rate of spread. Liebhold et al. (1992) identified three distinct periods where expansion velocity has varied: 1) high velocity (9.8 km/yr) from 1900 to 1915, 2) a low velocity (2.8 km/yr) from 1916 to 1965, and 3) a higher velocity (20.9 km/yr) from 1966 to 1990. These velocities were estimated from the relationship between a county's first record of infestation and its distance from the initial area of infestation. As infestation

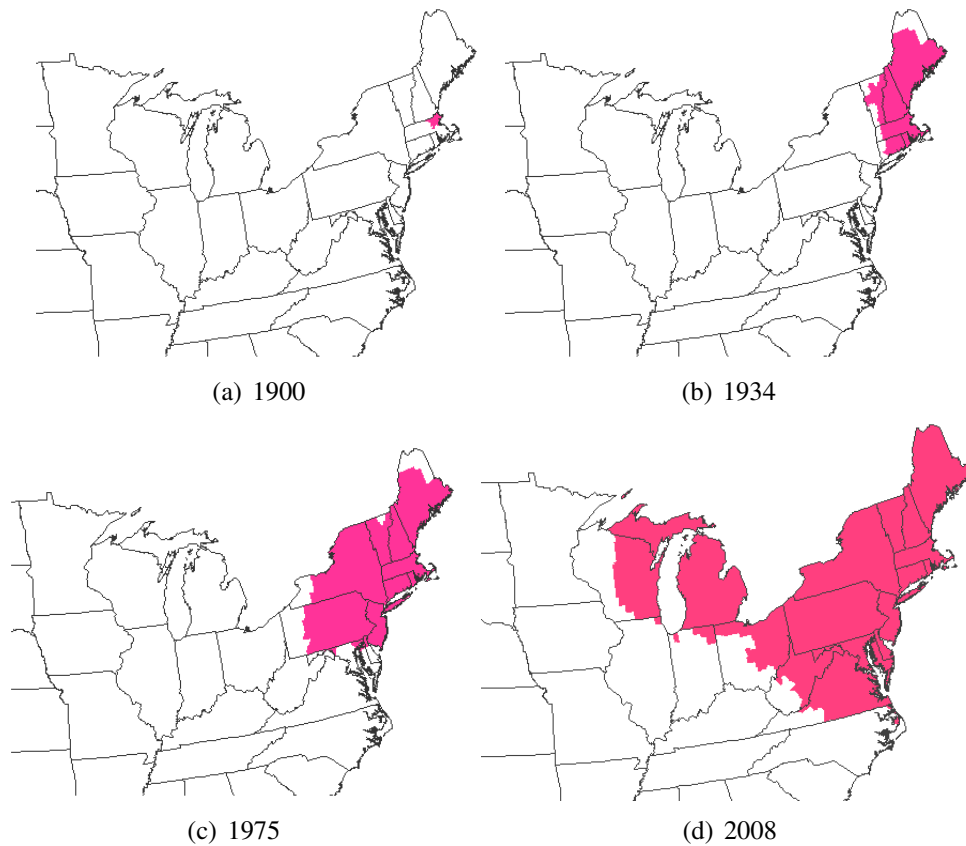


Figure 4.2: Gypsy moth infestation spread 1900-2008. (Liebhold 2003)

continues to spread at an alarming rate, synchronized outbreaks become more and more devastating to forests.

More precise maps combine data layers to show defoliation frequency. Figure 4.3 allows us to visualize more accurate areas of defoliation. While gypsy moth infestations continue to spread, defoliation will continue to be more damaging in areas where they have been established for longer. Areas where the gypsy moth has only invaded recently have a lower defoliation frequency at the moment.

We can see from Figure 4.3 that the gypsy moth has established itself in northern Virginia, and infestation has continued to spread to cover a good portion of the state. State management programs are likely to find local maps more beneficial. The Virginia Department of Forestry has data available for download containing information about gypsy moth defoliation from 2000 through 2009. We can use ArcGIS to project this data. All data was projected to North American Datum of 1983 (NAD83) using Lambert Conformal

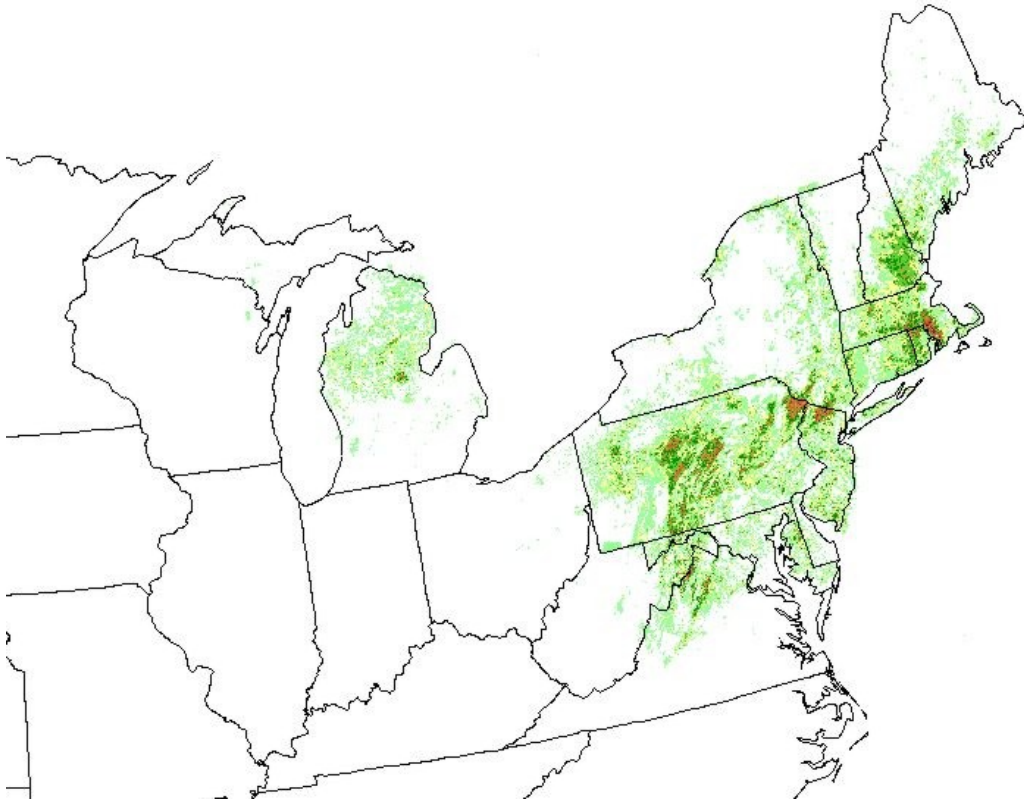
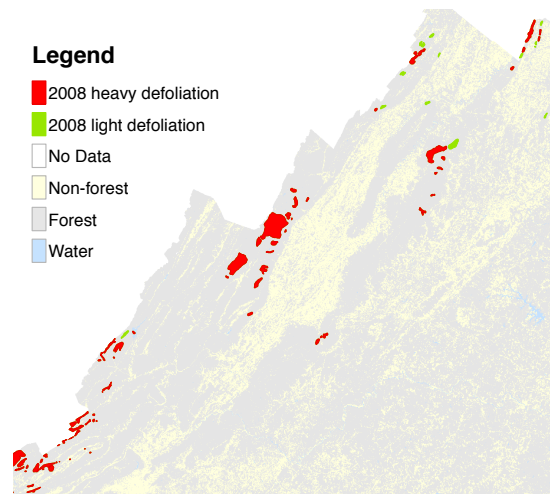
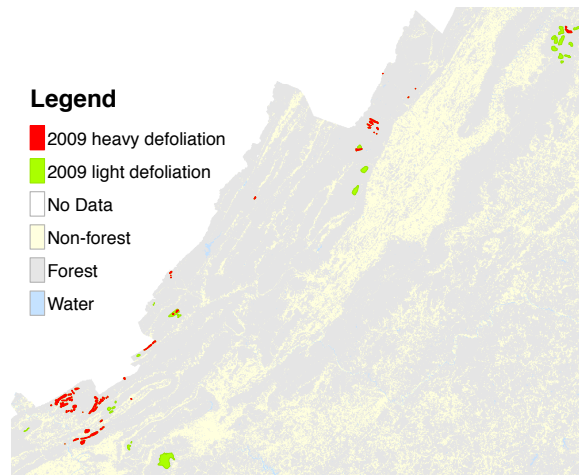


Figure 4.3: Gypsy moth defoliation frequency 1975-2002 scaled from highest (red) to lowest (light green). (Liebhold 2003)

Conic. Data from 2004 was not available for download. A Level 1 classification of the Virginia Forest Cover Map is used for geographical reference, also projected to NAD83. Since GIS is by definition a collection of geographically referenced data, we can extract desired information from an attribute table associated with each feature class or data layer. Maps contain information about the frequency and severity of gypsy moth defoliation. An attribute query may be done to highlight those inputs with heavy defoliation. Next, data is extracted to create a new feature class. Since data collection varies from year to year, data distinguishing between heavy and light defoliation is not always available. We perform attribute queries on gypsy moth defoliation data from 2008 and 2009 to create separate layers based on defoliation frequency. Figures 4.4(a) and 4.4(b) use data from Virginia Department of Forestry to differentiate between areas of high gypsy moth defoliate frequency and low gypsy moth defoliation frequency. Areas of high frequency typically indicated well-established colonies of gypsy moths.



(a) 2008 gypsy moth defoliation frequency.



(b) 2009 gypsy moth defoliation frequency.

Figure 4.4: Northern Virginia gypsy moth defoliation frequency, high vs. low.

From here, data on gypsy moth defoliation can be used to determine associations with specific forest types and elevations. Twenty different tree species have been identified as preferred host species for gypsy moths (Liebhold et al. 1995). This data was used to create maps of forest susceptibility to gypsy moths. In order to plan for management and prevention methods of gypsy moths in the future, it is necessary to identify the distribution of susceptible stands that are currently uninfested. There are already a number of sources for maps of susceptibility. The USDA forest service makes them easily accessible to the public. We see from Figure 4.5 that most of the susceptible stands exist in the eastern US, making that the region of greatest concern.

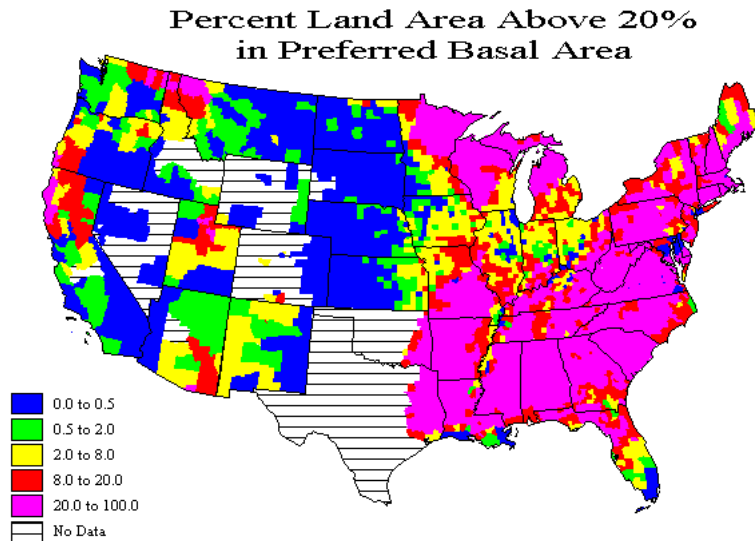
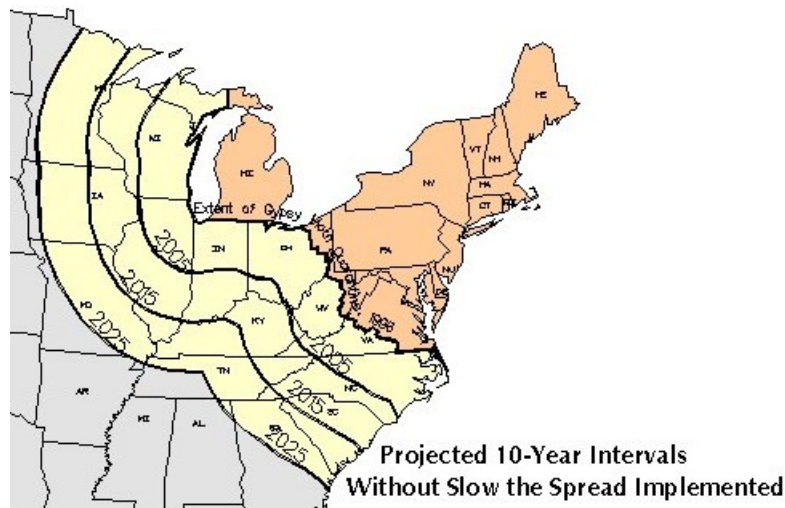


Figure 4.5: Forest susceptibility to gypsy moth invasion where over 20% of the basal stands are considered highly susceptible to gypsy moth invasion. (Liebhold 2003)

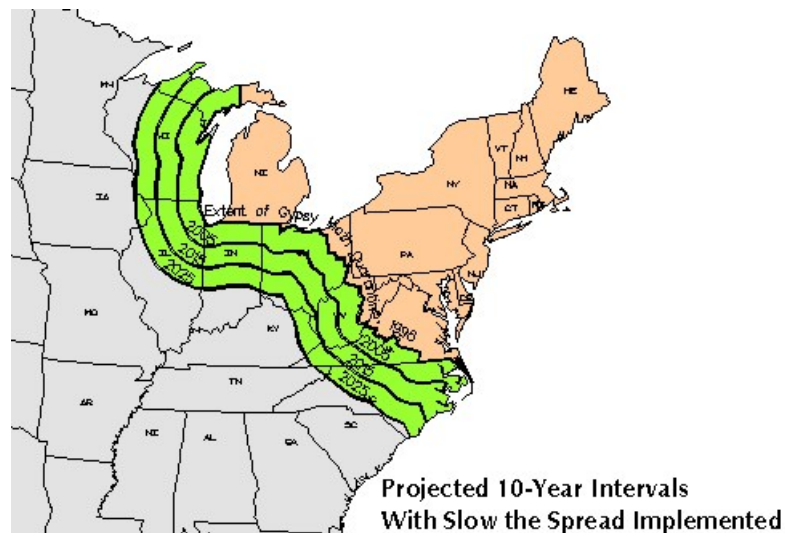
Slow the Spread

The Slow the Spread Foundation (STS) became funded by Congress in 2000. Since then, 11 states have worked in cooperation with the USDA Forest Service to implement a region-wide strategy to minimize the expansion rate of gypsy moths into currently uninfested areas. States work together to collect data necessary to project management. Spread has decreased substantially as a direct result of implementations from this programs. STS has been able to reduce the annual spread to just 3 miles per year, down from 13 miles per year. In the future, this will prevent defoliation of an extraordinary amount of susceptible forest area. Figure 4.6 compares the projected 10 year spread intervals with and without STS.

STS focuses on the transition areas between infested regions and areas that are in imminent danger of becoming infected. Gypsy moth populations in these areas are typically patchy and not yet well-established. Sharov and Liebhold (1998) identify three distinct zones that should be of greatest concern: the infested zone, the transition zone, and the uninfested zone. They used the idea of meta-populations to develop a population spread model based on the rate of colony establishment and the number of individuals



(a) Projected 10-year intervals without Slow the Spread



(b) Projected 10-year intervals with Slow the Spread

Figure 4.6: Projected 10-year intervals of gypsy moth spread with and without slow the spread. Implementations from the Slow the Spread Foundation are expected to minimize the spread of gypsy moths substantially. (Liebhold 2003)

in a colony. They used this model to predict the benefits of controlling the spread along what they referred to as the "barrier zone", or transition zone (Sharov and Liebhold 1998). Their model predicted that eradication of isolated, patchy, colonies in the STS project would reduce the spread rate by over 50%. The project implemented by STS has developed thorough data management and trapping protocols that each state adheres to in order to conduct intensive monitoring with pheromone-baited traps. Traps are used to detect isolated or low frequency populations in the transition zone. Data collected from intensive monitoring is then used in a decision-making algorithm designed to help determine the

most appropriate means of management (Slow the Spread of the Gypsy Moth 2012).

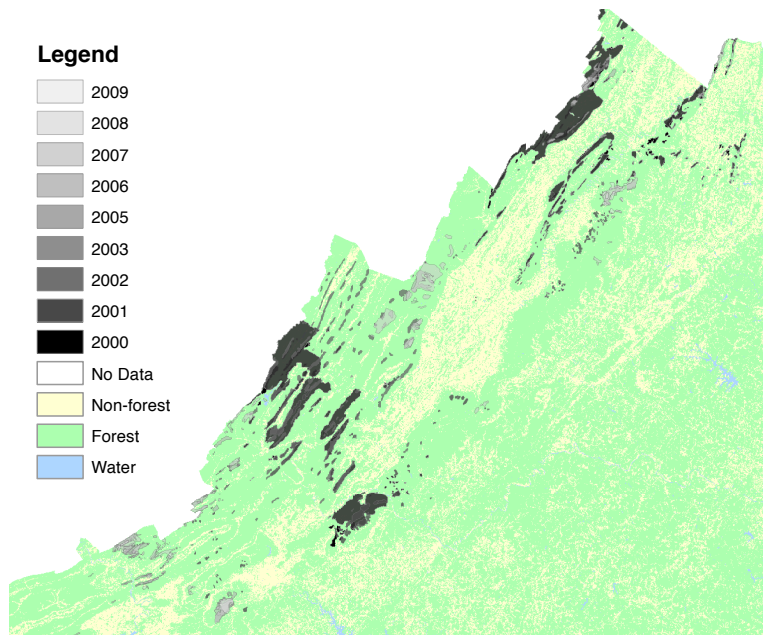
Notice from Figure 4.7 that once the gypsy moth invades, infestation radiates outward at an alarming rate. Figure 4.7(a) clearly displays gypsy moth expansion across northern Virginia. Darker shades of gray represent earlier gypsy moth defoliation, and lighter shades represent more recent defoliation. From Figure 4.7(b) we can see that defoliation was severe in 2001, but even though it spread in subsequent years defoliation became less severe and more patchy. This is due at least in part to recent management efforts along these transition zones.

STS prides itself in the use of environmentally friendly management tactics. All treatments are specific to gypsy moths, and they do not harm other species. They work to disrupt the natural progress of population spread. Some strategies include mating disruption, mass trapping, and spraying or a naturally occurring virus that attacks the internal tissue of gypsy moths (Gypchek). Gypsy moths are capable of causing extreme damage to our already threatened environment. Fortunately, with the help of foundations such as STS and modern technologies we can strive to prevent what could be nationwide defoliation.

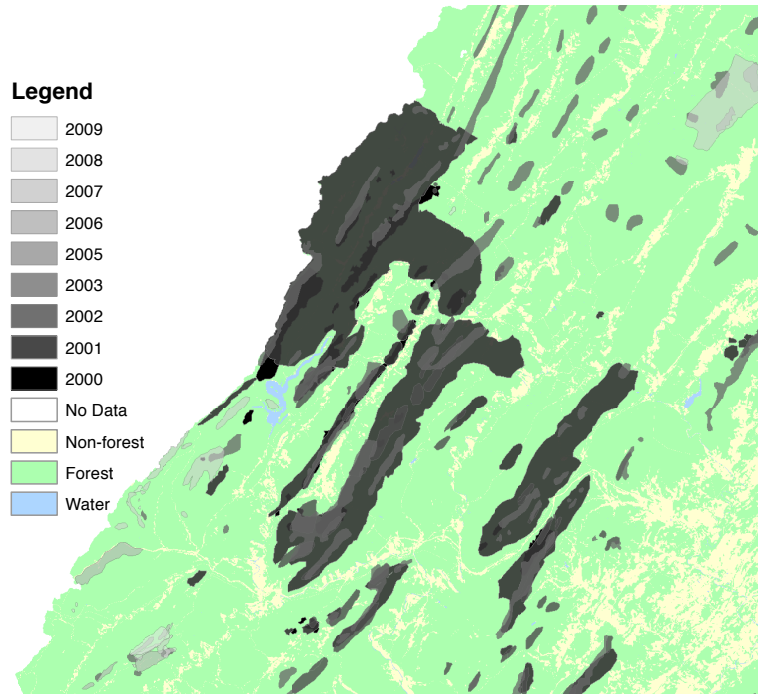
4.3 Discussion

Almost all aspects of ecology are somehow interconnected. Here, we saw how dynamics related to IGP ultimately lead to severe defoliation problems in the Eastern United States. The use of GIS is a more visual and data based technique, compared to mathematical analyses, that is used for conservation and management efforts.

IGP is extremely prevalent in nature, and the associated dynamics often have far-reaching effects. Gypsy moth defoliation is an example of how a thorough understanding of dynamics would prove beneficial to prevent continued damage. Mathematical modeling gives us a way to essentially translate nature into mathematical equations that are universally understood. We derived our models based on specific assumptions that would explain and predict changes in population biomass of a three species IGP subsystem. Models could also be used to help understand spatial synchrony of meta-populations and the



(a) Gypsy moth defoliation in Northern Virginia, 2000-2009.



(b) Gypsy moth defoliation has become patchy as they continue to spread into Virginia.

Figure 4.7: Northern Virginia gypsy moth defoliation 2000-2009.

rate of spread. Abbott and Dwyer (2008) found that synchrony in their model was due to correlations in the environmental conditions that affected the complex dynamics of multi-species subsystems. Model dynamics vary between single-species and multi-species systems. This is because single species systems do not include the complexity found in nature

due to species interactions. Thus, models that do not include the effects of IGP will fail to accurately predict species behavior.

The analysis of our continuous time-series model provides sufficient conditions for the persistence and extinction for all possible scenarios. Results indicate the controlling factors for our specific IGP subsystems with either generalist or specialist predators. Our models allow us to gain the insight into how our system will behave either over time or at equilibrium. The ultimate conclusions drawn from analyses are based on biological relevance, and a mathematical analysis is essentially useless without biological implications. If a model fails to accurately describe system dynamics then there may be problems with model assumptions or over-simplification of nature. While ours is a general model for three species IGP, we are able to gain insight into the dynamics that cause situations such as gypsy moth defoliation. Problems facing our environment are caused by the complicated dynamics of species interactions, and once we understand the driving forces it becomes easier to solve these problems.

Conservation biologists work adamantly to prevent ecological changes that lead to species extinction, ecosystem damage, and other problems facing our environment using knowledge from analyses. Analyses and simulations allow us to expand current biological theory to form new hypotheses and create new studies. We use models as tools to predict the effects of conservation efforts while simulations give us a visual display of potential dynamics over time. This way we can see when our efforts will begin to work and how the system is likely to behave before they begin to work.

Similar to mathematical models and simulations, GIS provides visual representations that can be used as a form of risk assessment. Spatial analyses allow us to apply geographically referenced data to various biological situations. We have focused on a three species IGP model based on the assumption that the IG prey is an insect with respective life cycles. Thus, we showed how GIS has been used in insect ecology to both compile data to keep track of trap records, egg densities, and defoliation and to categorize habitat susceptibility to future outbreaks. Spatial models are derived based on data, and they can

be used to predict the effects of conservation and prevention methods.

Future research will strive to extend current IGP models into multiple patch models in heterogeneous environments for synchronization analyses. We can consider the rate of establishment and growth of a new patch by adding a specific spatial component to our models. Patches typically occur at a transition zone in between infested and uninfested areas. The faster gypsy moths establish themselves in new patches, the faster the entire population front will spread. The new colonies grow and connect, ultimately contributing to the population front. Sharov and Liebhold (1998) estimate the rate of spread from two functions: (1) colonization rate as a function of the distance from the population front and (2) population numbers in a colony as a function of colony age. They were then able to target isolated colonies for eradication. This can be done with our model by adding a term for abundance at a specific location and rate of spread. By using a semi-discrete model, we can include stage-effects.

We could look at our system in terms of dispersal. Gypsy moths disperse long distances by means of accidental transportation and short distances by means of wind. We can include both long and short dispersal of gypsy moths in our models by adding a dispersal coefficient to gypsy moth populations. Then only a fraction of gypsy moths that disperse will establish new patches. A model that includes both population growth and spatial components is useful in predicting the rate of spread and establishment, facilitating the management effort. Once we can predict the rate at which the gypsy moth is likely to spread and the location that it is most likely to invade, eradication can be targeted.

Further analyses will use semi-discrete IGP model and species persistence/extinction to identify optimal conditions for permanence in an ever-changing environment. Considering current environment issues, it would be beneficial to incorporate weather effects, specifically climate change, into semi-discrete IGP model. By considering the addition of a spatial component this model could identify how climate change could affect the spatial and temporal distribution of species. We would also like to develop GIS spatial model that includes vegetation dynamics, nutrient states, soil components, and geographical struc-

tures to study how these affect the spread of gypsy moths as well as other pests

Analyses, whether they be mathematical or spatial, have proved promising for the future of conservation biology along with many other fields of mathematical biology. Models, simulations, and visual representations allow us to target and limit our efforts so we are not blindly attempting to alter our ecosystems.

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